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Revision of the Euphorbia polycarpa group of the Southwestern United States and adjacent Mexico; a preliminary treatment

LOUIS C. WHEELER

(concluded)

10. EUPHORBIA SETILOBA Engelm., ex Torrey, Pacif. Rail. Rep. 5: 364. 1857. *Chamaesyce setiloba* (Engelm.) Millsp., in Parish, Carn. Inst. Pub. 193: 6. 1913. *Chamaesyce setiloba* (Engelm.) Norton, Con. U. S. Nat. Herb. 25: 345. 1925. *Euphorbia floccosiuscula* Jones, Con. West. Bot. 15: 145. 1929.

Annual, with microscopically smooth tapering hairs throughout; stems slender, prostrate or perhaps rarely erect, rarely forming mats, internodes up to 2 cm. long, often much shortened toward the stem tips congesting the leaves and involucres into dense small "heads"; leaf blades 2–5 mm. long, oblong or oblong-ovate, base slightly oblique, petioles up to 1 mm. long; stipules not apparent; peduncles up to 1.5 mm. long, clothed as the herbage, filiform; involucres solitary in the axils, very shortly hairy without, glabrous within, long turbinate, constricted above, ca. 1.2 mm. long, ca. 1 mm. in diam.; lobes narrowly deltoid, entire, ciliate, equaling the glands; glands red, transversely oblong or the distal sometimes discoid, concave, 0.1–0.2 mm. long; appendages white, glabrous, ca. 1 mm. long and wide, parted into 3–5 narrow attenuate segments; fifth gland totally absent, its sinus depressed halfway to base of the involucre; bracteoles reduced to one filiform appendage adnate below to the involucre opposite each gland, with few or no hairs, free portion only ca. 0.2 mm. long; andropeds glabrous, ca. 1.2 mm. long, ca. equaling the glands, 3–7 per involucre; gynoped glabrous or with a few hairs above; ovary three-lobed, long white hairy, styles glabrous, 0.4–0.5 mm. long, parted to the base, clavate, slender; capsule long-hairy, spheroid, ca. 1.1 mm. long, sharply angled, capsule axis persistent; seeds 0.9–1 mm. long, quadrangular, sharply angled, facets with low irregular wrinkles, base truncate, ovate acutish radially, coat microreticulate, white but the brown testa showing through.

Type locality: Fort Yuma, Imperial Co., California. Distribution: southeastern California, Arizona, Lower California, Sonora, Sinaloa. Representative specimens seen: CALIFORNIA: Inyo Co.: Shepherd's Canyon, Argus Mts. *Jones in 1897* (P, F, D). San Bernardino Co.: 3 mi. N Cave Spring, Mohave Desert, *Peirson 8705* (Peir). Riverside Co.: Corn Spring, *Jones in 1926* (P); Dos Palmas, Colorado Desert, *Jaeger in 1921* (Peir); Riverside Mt., Colorado River, *Grinnell in 1910* (C). San Diego Co.: Mt. Springs, *Parish 9034* (D). Imperial Co.: *Major Thomas*, without loc. or date but probably from Fort Yuma (G, fragment of type?); 20 mi. NE Ogilby, *Munz & Hitchcock 12153* (P, C). ARIZONA: Mohave Co.: Kingman, *Braem in 1927* (D); Hackberry, *Rusby in 1883* (F, C). Coconino Co.:

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Williams Fork, *Palmer 514 in 1876* (G). Yuma Co.: Quartzsite, *Jones 24880* (UCLA, C, G, CA, P). Gila Co.: Sierra Ancha, *Harrison & Kearney 8292* (P). Pinal Co.: Apache Junction, *Gillespie 8432* (C). Pima Co.: Santa Catalina Mts, *Lemmon in 1880* (F, C), *in 1881* (C); Tucson, *Sherff in 1908* (F, C), *Jones in 1903* (P). Greenlee Co.: San Francisco Mts. near Clifton, *Greene in 1880* (F). Cochise Co.: Apache Pass, Chiracahua Mts., *Lemmon in 1881* (C). LOWER CALIFORNIA: Santa Rosalia, *Ferris 8698* (D, P), *Jones 22618 in part* (P); Purisima, *T. S. Brandegee in 1889* (F, C); Los Angeles Bay , *Palmer 629 in 1887* (G, 2 sheets, one sheet labeled Guaymas, but this is doubtless in error as Watson, Proc. Am. Acad. **24**:75. 1889, in a list of plants collected by Palmer, gave this number as from Los Angeles Bay). SONORA: no loc., *Pringle in 1884* (F, G); Hermosillo, *Jones 22739* (P, type of *Euphorbia floccosiuscula* Jones), *Rose, Standley & Russell 12494* (F); Guaymas, *Palmer 185½ in 1887* (F, G). SINALOA: San Blas, *Rose, Standley & Russell in 191-* (F); Fuerte, *Rose, Standley & Russell 13540* (F).

Palmer's 185½ from Guaymas is atypical in having longer internodes, larger leaves, and less deeply cut appendages than usual.

11. EUPHORBIA PETRINA Wats., Proc. Am. Acad. **24:** 75. 1889. *Chamaesyce petrina* (Wats.) Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia polycarpa* Benth. var. *petrina* (Wats.) Johnston, Proc. Cal. Acad. Sci. IV **12:** 1072. 1924.

Annual or perennial, prostrate, sometimes forming mats 30 cm. across; stems with fine spreading hairs, sometimes glabrate in age, internodes up to 1.5 cm. long, greatly shortened at the stem tips thereby congesting the leaves and involucres; leaves finely pubescent, blades entire, ovate, base markedly oblique-cordate, less oblique in the reduced upper leaves, 2–5 mm. long, juvenile leaves often much larger, variable in shape, subentire, petioles less than 1 mm. long; stipules minute, obscured by the pubescence of the stem; peduncles pubescent, less than 1 mm. long; involucres solitary in the axils, less than 1 mm. diam., short campanulate, cuneate to the peduncle, pubescent without, glabrous within except on the lobes, green veined opposite the lobes; lobes triangular, densely hairy, shorter than the glands; glands transversely oblong, 2–3 times longer than wide, up to 0.3 mm. long, red, mostly exappendiculate, or with very narrow white crenate appendages; fifth gland absent; sinus broadly V-shaped, slightly depressed; bracteoles reduced to one radial appendage adnate for half its length to the involucre opposite each gland, linear, parted to the middle, hairy above, ca. two-thirds as long as the andropeds; andropeds ca. 5 per involucre, glabrous, ca. 1 mm. long, barely equaling the glands; gynoped hairy above, exserted and reflexed at maturity; ovary three-angled, white hairy, styles bifid, glabrous, ca. 0.3 mm. long;

capsule glabrate on sides of the carpels, ca. 1.25 mm. diam., ca. 1 mm. long, axis persistent after dehiscence; seeds quadrangular, ca. 0.9 mm. long, ca. 0.6 mm. tangentially, ca. 0.5 mm. radially, ovate radially, base concave-truncate, facets convex, with gentle low irregular transverse ridges, white coat very thin, the brown testa showing through.

Type locality: San Pedro Martir Island, Lower California. Distribution: southern Lower California, Sonora, Sinaloa. Specimens seen: MEXICO: Lower California: San Pedro Martir ("Martin") Island, *Palmer 412 in 1887* (G type, C, F on copied label loc. is "Maleja, Lower Calif."). San Esteban, *T. S. Brandegee 39 in 1889* (F, C). Sonora: Alamos, *Rose, Standley & Russell 12900* (F). Sinaloa: Fuerte, *Rose, Standley & Russell 13453* (F); San Blas, *Jones 23313* (P, C, CA, G); Culiacan, *T. S. Brandegee in 1904* (C), *Palmer 1808 in 1891* (G).

12. EUPHORBIA LAREDANA Millsp., Pittonia **2**: 89. 1890. *Chamaesyce laredana* (Millsp.) Small, Fl. SE U. S., 709. 1903.

Prostrate annual; plant more or less tomentose throughout; stems several, 10–20 cm. long, stout (1.5 mm. diam.) toward the base, internodes to 1 cm. long; leaf blades extremely oblique even to the small upper ones, ovate (distorted by the obliquity) 3–5 mm. long, margin entire or the large juvenile leaves with a few low discrete teeth, petioles less than 1 mm. long; stipules minute and obscured by the tomentum; peduncles ca. 0.5 mm. long; involucres solitary in the axils, tomentose without, glabrous within except above, short campanulate, cuneate to the peduncle, 1 mm. or less diam., green veined opposite the lobes; lobes deltoid, equaling or slightly exceeding the glands, hairy; glands transversely oblong, 0.2 mm. long or shorter, yellowish; appendages absent or very narrow; fifth gland absent; sinus slightly depressed and with long hairs; bracteoles reduced to one radial appendage opposite each gland, adnate to the involucre for half its length, entire to one or two-parted to the base, hairy above; andropeds 5 or fewer per involucre, glabrous, 1 mm. long, included; gynoped tomentose above, glabrous below, exserted and reflexed at maturity; ovary sharply three-angled, tomentose, styles bifid, less than 0.2 mm. long; capsule glabrate on the sides of the carpels, the backs usually persistently tomentose, sharply three-angled, 1.5 mm. long, 1.5 mm. diam; seeds sharply quadrangular, narrowly ovate radially, base concave-truncate, facets concave, with irregular white farinose transverse ridges including the angles, 1.1–1.2 mm. long, 0.5 mm. radially and tangentially; capsule axis persistent.

Type locality: Laredo, Webb Co. Texas. Distribution: Known only from the type locality. Specimens seen: TEXAS: Webb Co.: Laredo, *Pringle 2074* (F, type), *2070* (G), *Reverchon 3786* (P, G), *Pringle 3747* (C, F, P, G).

13. EUPHORBIA MICROMERA Boissier, DC. Prod. 15[2]: 44. 1862. *Chamaesyce micromera* (Boiss.) Wooton & Standley, Contr. U. S. Nat. Herb. 16: 144. 1913. *Euphorbia pseudoserpyllifolia* Millsp., Pittonia **2**: 87. 1890. *E. pseudoserpyllifolia* forma *typica* Howell, Leafl. West. Bot. 1.52: 1933. *E. pseudoserpyllifolia* forma *villosa* Howell, Leafl. West. Bot. 1: 53. 1933. *Chamaesyce pseudoserpyllifolia* Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia podagrica* Johnston, Univ. Calif. Pub. Bot. 7:440. 1922.

Prostrate annual; stems glabrous or pubescent, extremely variable, one extreme very straight, thick, with thickened nodes, and internodes up to 1 cm. long, the other extreme flexuous or straightish, slender, nodes not thickened, internodes up to 2 cm. long; leaves glabrous or short pubescent, blades 2–7 mm. long, ovate and base markedly oblique in the larger, oblong and base slightly oblique in the smaller, petioles ca. 0.5 mm. long; stipules ca. 0.75 mm. long, or shorter in pubescent plants, triangular, ciliate, upper distinct, lower often united toward stem tip; peduncles glabrous or pubescent, up to 1 mm. long; involucres solitary in the axils, ca. 1 mm. in diam., very short campanulate, narrowed above, more or less cuneate to the peduncle, glabrous or pubescent without, glabrous within except the lobes, green veined opposite the lobes; lobes deltoid, equaling or slightly exceeding the glands, hairy within; glands pink or red, strictly discoid or slightly transversely elongate, especially the proximal, 0.1–0.15 mm. diam.; appendages absent; fifth gland absent; sinus broadly V-shaped, hairy, little depressed; bracteoles reduced to a solitary linear hairy appendage ca. 0.5 mm. long, adnate for most of its length to the involucre opposite the glands; andropeds mostly 5 per involucre, glabrous, included, barely 1 mm. long; gynoped glabrous throughout or short hairy above, long-exserted and usually reflexed at maturity; ovary three-angled, glabrous to pubescent, carpels slightly grooved on the back; styles bifid, glabrous, 0.1 mm. long; capsule three-angled, glabrous or glabrate, spheroid, ca. 1.3 mm. long; seeds quadrangular, 1.1–1.3 mm. long, 0.5 mm. tangentially, 0.4 mm. radially, narrowly ovate radially, angles sharp, facets smooth or with very faint wrinkles, convex, expecially the front, base truncate, raphe straight or slightly concave, shortly truncate at a slight angle above, microreticulate white coat thin, with the brown of the testa showing through.

Type locality: New Mexico. Distribution: deserts of Nevada, California, Arizona, New Mexico, northern Lower California, and Coahuila. Specimens seen: NEVADA: Co.?: Gold Mt., *Purpus 6437 in part* (C, type of *Euphorbia podagrica* Jtn.). Mineral Co.: Sodaville, *Brandegee Herb. (collector?) in 1912* (C). CALIFORNIA: Inyo Co.: Owens Lake, *Purpus 3046* (C); Darwin Mesa, *Hoffmann in 1931* (SB). Los Angeles Co.: Rosamond, *collector not stated, in 1929* (SB). Riverside Co.: Colorado Desert: Salton Bench Mark, *Wheeler 369* (W, P, Peir); Desert Center, *Jones 24879* (UCLA, C, CA, P in part); Cathedral City, *Howell 6651* (CA, type

of *Euphorbia pseudoserpyllifolia* Millsp. forma *villosa* Howell). San Diego Co.: San Felipe Valley, *Hoffmann in 1929 in part* (SB). Imperial Co.: between Brawley and Salton Sea, *Parish 8301* (G, D, F "SW Brawley" on the label); Colorado River bottoms at Fort Yuma, *Parish 8307* (D, F). ARIZONA: Co.?: Gila River Valley, *Mohr in 1873* (F, type of *Euphorbia pseudoserpyllifolia* Millsp.). Mohave Co.: Yucca, *Jones in 1884* (P). Yuma Co.: Quartzsite, *Jones 24874* (P, CA). Maricopa Co.: Gila Bend, *Harrison & Kearney 7990* (F). Pinal Co.: Casa Grande, *Jones in 1884* (P). Greenlee Co.: San Francisco Mts. near Clifton, *Greene in 1880* (F). Cochise Co.: Bowie, *Jones 4223* (P, F marked "type" of *Euphorbia pseudoserpyllifolia* Millsp. by Millspaugh). NEW MEXICO: Co.?: no loc., *Wright 1854*, type collection of *E. micromera*, (G, F) Doña Ana Co.: 3 mi. W. La Mesa, Mesilla Valley, *Fosberg S4024* (P). MEXICO: Coahuila: Nassus River, Torreon, *Palmer 494 in 1898* (F, C). Lower California: Socorro, northern Lower Calif., *Orcutt 1331 in 1886* (F, G, C, D).

The inclusion of plants with stout stems and thickened nodes and pubescent herbage, and with slender stems and glabrous herbage in one entity is the only course which will not result in chaos, for all combinations of these vegetative characters occur. The reproductive and associated organs are very uniform and distinctive.

14. EUPHORBIA LATA Engelm. in Torr., Mex. Bound Survey, 188. 1859. *Chamaesyce lata* (Engelm.) Small, Fl. SE U. S., 1333, 1903. *Euphorbia dilata* Torr. & Gray, Pacific Rail. Rep. II 2: 175. 1861, not Hockst. or E. Mey. *Euphorbia rinconis* Jones, Con. West. Bot. 12: 76. 1908.

Perennial; stems ascending or erect, 10–15 cm. long, 0.5–1 mm. thick, with appressed short hairs, internodes 0.5–2 cm. long; leaves with short appressed hairs, blades ovate-deltoid-falcate to long deltoid or virtually linear in some cases by revolution of the margins, margin entire, more or less revolute, petioles ca. 1 mm. long; involucres solitary in the axils, turbinate, 1.75–2 mm. in diam., with short appressed hairs without, glabrous within except above; lobes deltoid, entire, equaling or exceeding the glands; glands transversely oblong, ca. 0.5 mm. long, hairy beneath; appendages absent or very narrow, white, crenate; fifth gland minute or absent, with a tuft of hairs in its interval; sinus somewhat depressed; bracteoles united below into one radial appendage adnate below to the involucre opposite each gland, 4–7 parted above, not quite equaling the glands, with straight long slender hairs above; andropeds 5–7 per fascicle, 25–35 per involucre, equaling the glands, with numerous hairs above; gynoped hairy, shortly exserted and reflexed at maturity; ovary with short appressed hairs, three-angled, styles ca. 0.75 mm. long, parted to or below the middle, with very short hairs below; capsule sharply three-lobed, with appressed hairs, ca. 2.5 mm. long, 2.5 mm. diam.,

axis persistent after dehiscence; seeds quadrangular, 2 mm. long, 1 mm. radially and tangentially, long-deltoid radially, back rounded, face straight in tangential silhouette, base obtuse-truncate, angles sharp, facets smooth, depressed, coat white, microreticulate.

Type locality: "Western Texas." Distribution: plains of Colorado and Kansas southward into Coahuila, Mexico. Representative specimens seen: COLORADO: Bent Co.: Las Animas, *Osterhout 3923* (P). NEW MEXICO: *Fendler 794* (F, G). Doña Ana Co.: Rincon, *Jones in 1890* (P, type of *Euphorbia rinconis* Jones); S of the White Sands, *Wooton in 1899* (C, D, P). Chaves Co.: 20 mi. S Roswell, *F. S. & E. S. Earle 284* (P). TEXAS: Culberson Co.: Van Horn, *Jones 26019* (P). Reeves Co.: Pecos, *Hanson 780* (G), *Tracy 104* (G). Crockett Co.: Ozona, *Jones 26015* (W). Tom Green Co.: San Angelo, *Reverchon 3795* (G), *Palmer 10310* (D). Runnels Co.: Ballinger, *Neally in 1889* (F). Midland Co.: Midland, *Tracy 7448* (F). Mitchell Co.: Colorado City, *Oyster in 1883* (F). Lubbock Co.: Lubbock, *Demaree 7560* (G, D). Potter Co.: Amarillo, *Neally in 1888* (F). Hall Co.: Estelline, *Reverchon 4303* (P). OKLAHOMA: Texas Co.: Camp, *Stevens 406* (G), *403* (G). Beaver Co.: 15 mi. SW Beaver City, *Stevens 349* (G, D). Harmon Co.: Hollis, *Stevens 1067* (P, D, G). KANSAS: Grant Co.: Ulysses, *Thompson 20* (G, C). Trego Co.: no loc., *Hitchcock 474* (G). MEXICO: Coahuila: Peña, *Purpus 1098* (C); Novano, *Purpus 4511* (C); San Lorenzo de Laguna 22–27 leagues SW Parras, *Palmer 1205 in 1880* (F).

The collections from Mexico are atypical in that the leaves are not falcate and the margins are plane but the hairs are present on the andropeds and the seeds are typical.

The collection: 15 mi. N Magdalena, Sonora Mex., Fosberg 7430 (UCLA); reported by Fosberg & Ewan, Bull. So. Cal. Acad. Sci. **34:** 178–179. 1935, as the first record of *E. lata* from Sonora, is *E. pediculifera* var. *typica* and is cited under that species.

15. EUPHORBIA ACUTA Engelm., Bot. Mex. Bound., 189, 1859. *Chamaesyce acuta* (Engelm.) Millsp., Field Mus. Pub. Bot. 2: 407. 1916. *Euphorbia acuta* Engelm. var. *stenophylla* Boiss., DC. Prod. **15**[2]**:** 18. 1862.

Perennial from a taproot as much as 1 cm. thick; stems annual, erect or ascending, numerous, 10–30 cm. long, to 1.5 mm. diam., with long weak hairs partially deciduous in age, internodes 1–4 cm. long; leaves sessile or subsessile, sparingly long villous below, less so and glabrate above, mostly 1–2 cm. long, ovate-lanceolate to lanceolate, base sub-symmetrical, apex long-acuminate, cartilaginous at the extreme tip, margin sometimes strongly revolute; stipules apparently wanting; peduncles stout, to 2 mm. long, sparingly to densely

villous; involucres solitary in the axils, turbinate, 1.75–2.5 mm. diam., sparsely to markedly villous without, with fine short hairs within; lobes narrowly deltoid and entire, or broader and two-toothed, equaling or slightly exceeding the glands; glands transversely elongate, slightly concave, ochroleucous, the proximal 1–1.5 mm. long, the distal shorter; appendages mostly wanting, when present to a little wider and longer than the glands, glabrous, white, margin with irregular short blunt teeth; fifth gland totally absent; sinus somewhat depressed, U-shaped; bracteoles 3–5 opposite each gland, united at the base and sometimes throughout, of various lengths, some usually nearly equaling the glands, long hairy; andropeds 4–5 per fascicle, 20–25 per involucre, 2.2–2.5 mm. long, slightly exserted, with from few to numerous slender hairs throughout; gynoped hairy, exserted and reflexed at maturity; ovary densely white hairy, styles glabrous, ca. 1 mm. long, parted to the middle, divisions somewhat flattened, recurved; capsule sharply three-lobed, 3 mm. long and diam., short appressed-hairy, axis persistent; seeds quadrangular, ovate radially, 2.2–2.5 mm. long, 1.5–1.7 mm. tangentially, 1.5 mm. radially, base oblique, coat white, microreticulate.

Type locality: "W Texas along the San Pedro & Pecos Rivers." Distribution: New Mexico, Texas and Coahuila. Specimens seen: NEW MEXICO: Co.?: no locality, *Wright #1840* (G, F fragment of type of var. *stenophylla* Boiss.), *Wright 1739* (G). Eddy Co.: Hope *Jones 26013* (P); Carlsbad, *Benke 5034* (G, F). TEXAS: Rio Bravo del Norte, *Schott in 1852* (F); River Pecos, San Pedro, (sic on copied label) *Wright #1839* (F, apparently fragment of the type). Reeves Co.: Pecos City, *Neally in 1889* (F). Pecos Co.: Fort Stockton, *Whitehouse 8419* (F); Crockett Co.: Ozona, *Jones 26015* (P). Valverde Co.: Del Rio, *Jones 26014* (P). Uvalde Co.: Utopia, *Palmer 10228* (D); West of Uvalde, *Jones 28439* (C). MEXICO: Coahuila: 100 miles N Monclova, *Palmer in 1880* (G); Diaz, *Pringle 8278* (F, P, G, C).

16. EUPHORBIA PENINSULARIS Johnston, U. Calif. Pub. Bot. **7**: 440. 1922.

Annual; stems to 25 cm. long, ascending or erect, few to several from the base, reddish brown, sparsely tomentose, internodes of the main branches often 3–4 cm. long, consequently the habit lax; petioles ca. 1 mm. long, leaf blades entire, sparsely short appressed-tomentose, often reddish brown in age, of two sorts: the first thinnish, oblong, 1–3 cm. long, with very slightly revolute margin and markedly oblique base, on the main branches; the second thickish, narrower to often linear by extreme revolution of the margin, these mostly on short lateral branches; stipules ca. 0.5 mm. long, consisting of 3–5 sparsely hairy linear segments on either side of the stem; peduncles up to 1 mm. long, sparsely short tomentose; involucres congested in glomerules on short leafy lateral branches, campanulate, 1.5 mm. diam., with short spreading

hairs without, glabrous within except just below the glands and on the lobes; lobes deltoid attenuate, slightly exceeding the glands; glands transversely oblong, concave; appendages conspicuous, white, glabrous, mostly ca. 1 mm. wide and 2 mm. long; fifth gland absent, its sinus U-shaped and slightly depressed; bracteoles numerous, forming a radial appendage opposite each gland, bracteoles of each appendage united below and adnate to the involucre for almost the whole length of the outer bracteoles, more or less hairy above; andropeds ca. 4 per fascicle, 20 per involucre, ca. 1.5 mm. long, glabrous, slightly exserted; gynoped glabrous except above; ovary densely straight-hairy, very slightly lobed; styles glabrous, 0.7–0.8 mm. long, parted to below the middle, slender; capsule sparsely hairy, ca. 2 mm. long and diam., widest at base and tapering upwards, carpels acutish on back but angles between the carpels only very slightly reëntrant; seeds sharply quadrangular, ca. 1.4 mm. long; ca. 1 mm. tangentially, ca. 0.8 mm. radially, ovate radially, base truncate, facets concave, with slight transverse wrinkles, white coat very thin, the brown testa showing through.

Type locality: San José del Cabo, Lower California. Distribution: south end of Lower California. Specimens seen: San Antonio [of the seven odd towns by this name in Lower California this is evidently the southernmost judging by the itinerary, Con. West. Bot. 17: 13. 1930.] *Jones 22737 in 1926* (P); San José del Cabo, *Purpus 325* (C, type), *Purpus 7838* (G), *T. S. Brandegee in 1890* (C); Cape San Lucas, *Craig 629* (P).

17. **Euphorbia apicata** Wheeler n. sp.

Planta prostrata, perennis, cum capillis brevibus appressis crispisque praeter facies superiores foliorum; caulibus tenuibus, cum diametro minus 1 mm., internodis usque ad 3 cm. longis, ad summas brevioribus; stipulis dorsalibus ventralibusque ambis distinctis, linearibus, ca. 0.3 mm. longis; laminis foliorum integris, 3–7 mm. longis, ovato-oblongis, apice subacuto, base parum obliqua; petiolis ca. 0.5 mm. longis; pedunculis ca. 1 mm. longis; involucris in axilis solitariis sed in capitulis ad extremitates ramulorum plerumque congestis, involucris extra cum capillis paucis brevibus porrectis, intus glabris, cum diametro ca. 1 mm.; lobis glandulas leviter excedentibus, deltoideis, acutis, integris, cum capillis paucis brevibus porrectis in apice; glandulis nigropuniceis, transverso-oblongis, proximis ca. 0.5 mm. longis, distalis brevioribus; appendiculis conspicuis, glabris, albis, cum margine integra vel inaequaliter crenulata, usque ad 1.2 mm. longis et 0.5 mm. latis; glandula quinta ca. tertiom longitudinem sinus, late triangulare, cum capillis paucis porrectis; sinus late U-formato, leviter depresso; bracteolis quam andropedibus leviter brevioribus, 4–6 quaque glandula oppositis infra connatis et ad involucrum adnatis appendiculum radialem facientibus, parte libera bracteolarum cum capillis brevibus supra; andropedibus 4–5 in fasciculo singulo, 20–25 in involucro, glabris, leviter exsertis, ca. 1 mm. longis; gynopede

glabro (cum capillis paucis brevibus in apice), longo-exserto et in maturitate plerumque reflexo; ovario cum capillis leviter crispis brevibus; stylis prope ad basim partitis, tenuibus, leviter clavatis, glabris, ca. 0.3 mm. longis; capsula cum capillis paucis brevibus fere porrectis, distincte 3-angulata, dorsis carpellorum et linea conjunctionis carpellorum brunneis; seminibus debile albo-brunneis, radiale ovata-acutis, cum base truncata et depressa, ca. 0.8 mm. longis, tangentiale ca. 0.5 mm., radiale ca. 0.5 mm., seminibus quadrangularibus, angulis acris, lateribus planis, leviter rugulosis, apice cum mucrone brevissimo inflexo; axe capsulae persistente.

Type locality: Sierra de la Laguna, Lower California. Known only from the type: Sierra de la Laguna, [Lower] California, *T. S. Brandegee, Oct. 2, 1899* (C sheet #110779). Although the heading of the label reads "California" the locality Sierra de la Laguna is well known in Lower California and no such locality name seems ever to have been used in California. That T. S. Brandegee was in Lower California about the date the type was collected is evidenced by Brandegee's collection of *Agave Brandegei* Trelease made in Cape region mountains, Lower California, Sept. 20, 1899, cited by Trelease, Ann. Rep. Mo. Bot. Gard. **22**:57. 1911. In view of this evidence it seems reasonable to assume that Brandegee chanced to use the wrong label form for this *Euphorbia*.

In addition to the differentiae given in the key this species is distinguished from *E. peninsularis*, its nearest relative, by the shorter seeds and andropeds in *E. apicata*.

18. EUPHORBIA MELANADENIA Torrey, Pacif. Rail. Rep. 4: 135. 1857. *Anisophyllum melanadenium* (Torr.) Klotzsch & Garcke, Abh. Akad. Berl. 1859 (1860) 23. *Chamaesyce melanadenia* (Torr.) Millsp., Field Mus. Pub. Bot. 2: 410. 1916. *Euphorbia cinerascens* Engelm. var. *appendiculata* Engelm., in Torr., Bot. Mex. Bound., 186. 1859. *E. polycarpa* Benth. var. *appendiculata* (Engelm.) Munz, Bull. So. Cal. Acad. Sci. **31**: 68. 1932. *E. polycarpa* Benth. var. *vestita* Wats., Bot. Cal. 2: 73. 1880. *Chamaesyce aureola* Millsp., Field Mus. Pub. Bot. 2: 406. 1916.

Perennial from a taproot as much as 5 mm. diam.; stems ascending or erect, to 20 cm. long, sometimes stout (1.5 mm. diam.) below, closely tomentose, glabrate; leaf blades 2–5 mm. long, ovate to ovate-lanceolate, base oblique, closely and often hoary tomentose on both surfaces, petioles clothed as the leaves, mostly ca. 1 mm. long; ventral stipules mostly united, linear, hairy, to 1 mm. long, dorsal stipules distinct, linear, hairy, to 1 mm. long; peduncles less than 1 mm. long, with short appressed hairs; involucres solitary in the axils, open-campanulate, 1.25–1.5 mm. diam., appressed short hairy without, glabrous within except below the glands; lobes narrowly deltoid, copiously hairy, equaling the glands; glands transversely oblong, dark red-

dish; appendages usually conspicuous, twice as wide as and longer than the glands to rarely wanting, white, margin crenate to subentire, glabrous or rarely with a few short hairs beneath next to the gland; fifth gland absent; sinus U-shaped, not depressed, densely hairy; bracteoles more or less completely united into an upwardly broadening, densely hairy, thickish, radial appendage adnate on the lower half to the involucre opposite each gland; andropeds 3–4 per fascicle, 15–20 per involucre, 1.5–2 mm. long, glabrous or rarely with short hairs above; gynoped shortly appressed-hairy, exserted and reflexed at maturity; ovary copiously hoary-tomentose, roundly three-lobed; styles parted nearly to the base, 0.5–0.8 mm. long, short-hairy below, slender throughout; capsule 1.5–1.75 mm. long, ovoid, sharply angled, very short tomentose; seeds quadrangular, 1.25–1.5 mm. long, ca. 0.6 mm. radially, ca. 0.6 mm. tangentially, facets smooth or slightly wrinkled, apex acutish, coat white, microreticulate.

Type locality: "San Gabriel," California. Actually probably the foot of the San Gabriel Mts. a few miles north as this is a foothill plant. Distribution: southern California, southwestern Arizona, northwestern Lower California and Guadalupe Island. Representative specimens seen: CALIFORNIA: Los Angeles Co.: Santa Monica Mts. (Sierra Santa Monica): no locality, *Hasse in 1890* (F); Cahuenga Pass, *Brewer 178*(C); Coldwater Canyon, *Peirson 4441* (Peir). Griffith Park, Los Angeles, *Epling in 1925* (UCLA); La Tuna Canyon, Verdugo Mts. (Range), *Ewan 4169* (P, C, CA, UCLA, Peir); Pasadena, *Kennedy in 1893* (P); San Gabriel, *Bigelow without date or number* (F, fragment of type of *Euphorbia melanadenia* Torr.), *Brewer 171* (C, wrong number fide note on sheet); Azusa, *Smith 4933* (F, type of *Chamaesyce aureola* Millsp.); 2 mi. NE La Verne, *Wheeler 9* (W, CA, UCLA); San Gabriel Mts.: Arroyo Seco at 1250 ft., *Peirson 310* (Peir); Santa Anita Canyon, *Wheeler 2535* (W, P); Little Santa Anita Canyon, *Abrams 2633* (P, D); Rogers Canyon, *Wheeler 399* (W, UCLA); San Gabriel River, *Blake 892* (F); Liveoak Canyon, *Johnston 1806* (P, C); San Antonio Canyon, *Abbott in 1906* (P). San José Hills W Pomona, *Munz & Harwood 3289* (P, D), *3288* (P); Puente Hills S Pomona, *Munz, Street, & Williams 2288* (P, D). San Diego Co.: Palm Canyon, Borrego Valley, *Munz & Hitchcock 11338* (P); Box Canyon, Colorado Desert, *Munz & Hitchcock 12068* (C, P); Montezuma Valley near Warner's Hot Springs, *Jaeger in 1925* (C, P); Jacumba, *Munz 8079* (P), *Abrams 3660* (D); San Felipe, *Thurber 628* (F), *T. S. Brandegee in 1895* (C); Vallecito Canyon, Laguna Mts., *Peirson 4865* (Peir); Mountain Springs, *Ferris & Bacigalupi 8244* (C), *Jones in 1924* (P). Imperial Co.: Mountain Springs Grade, *Munz 11950* (P, C). ARIZONA: Mohave Co.: Hackberry, *Jones in 1884* (P, D). Yavapai Co.: Congress Junction, *Jones in 1903* (P, D). Maricopa Co.: Mammoth, *Neally 271* (F). Pinal Co.: Oracle, *Jones in*

1903 (P), *Eggleston 15950* (F). Gila Co.: Roosevelt Dam, *Goodding 717* (G). Pima Co.: Rincon Mts., *Blumer 3278* (F); Sabino Canyon, Santa Catalina Mts., *Thornber 216* (P, D, C). LOWER CALIFORNIA: El Llano de Santana, *T. S. Brandegee in 1889 in part* (C); El Rancho Viejo, *T. S. Brandegee in 1889* (F, C); Cantillas Canyon, *Orcutt 35* (F); San Quentin Bay, *Orcutt 2196* (F); Guadalupe Island, *Palmer 783 in 1889* (F, C).

The plant from Mt. Springs, San Diego Co., California, *Ferris & Bacigalupi 8244* (C) is atypical in having hairy andropeds. Likewise the collection: Santa Anita Canyon, San Gabriel Mts., Los Angeles Co., California, *Wheeler 2535* (W, P) also has hairy andropeds. As this collection was of very robust plants there may be a relation between the vigor of the plant and the presence of hairs on the andropeds. The "Cuphea-like" involucral galls occur on one collection from Arizona: Pima Co.: Rincon Mts., *Peebles & Kearney 8769* (F, P).

19. EUPHORBIA CINERASCENS Engelm., in Torr., Bot. Mex. Bound., 186. 1859. *Chamaesyce cinerascens* (Engelm.) Small, Fl. SE U. S., 710. 1903. *Euphorbia melanadenia* Torr. var. *subinappendiculata* Engelm., ex. Boiss., DC. Prod. **15**[2]: 32. 1862.

Perennial, forming mats up to 50 cm. in diam.; stems to 30 cm. long; prostrate or decumbent, mostly slender (1 mm. diam.), closely tomentose; leaf blades 2–5 mm. long, ovate with oblique base to oblong with slightly oblique base, usually glabrous above, closely tomentose beneath, petioles tomentose, mostly ca. 1 mm. long; stipules hairy, ca. 0.5 mm. long, ventral united, linear, dorsal distinct, linear; peduncles less than 1 mm. long, with short appressed hairs; involucres solitary in the axils, turbinate, 1.25–1.5 mm. diam., appressed short hairy without, glabrous within except below the glands; lobes narrowly deltoid, copiously hairy, equaling the glands; glands transversely oblong, dark reddish-purple; appendages narrow or usually wanting; fifth gland absent; sinus U-shaped, not depressed, densely hairy; bracteoles forming a radial appendage opposite each gland, often united only below, with 5 or 6 very slender short hairy free segments above; andropeds 3–4 per fascicle, 15–20 per involucre, 1.5–2 mm. long glabrous, gynoped shortly appressed-hairy, exserted and reflexed at maturity; ovary copiously hoary-tomentose, roundly three-lobed; styles parted nearly to the base, 0.5–0.8 mm. long, short-hairy below, clavate; capsule 1.5–1.75 mm. long, ovoid, sharply angled, very short tomentose; seeds quadrangular, 1.25–1.5 mm. long, ca. 0.6–0.9 mm. radially, ca. 0.6–1 mm. tangentially, facets smooth or faintly wrinkled, oblong or often deltoid-oblong radially (i.e. wider below), base obtuse or truncate, apex acutish, coat white, microreticulate.

Type locality: "On the Rio Grande," Texas. Distribution: southwestern Texas, south through Coahuila to Taumalipas and San Luis Potosi. Representative specimens seen: TEXAS: Co.?: no locality, *Wright 534 in*

1850 (F); along the Rio Grande, *Wright 559 in 1849*, type collection?, (F). Brewster Co.: Bouquillas, *Parks in 1929* (F); Chisos Mts., *Moore & Steyermark 3266* (C). Valverde Co.: Del Rio, *Palmer 12342* (C), *Jones 28463* (P, C), *25997* (P). Maverick Co.: Eagle Pass, *Jones 28464* (P). Dimmit Co.: Carrizo Spring, *Jones 28461* (P, C). Zapata Co.: San Ygnacio, *Tharp 3542* (P). MEXICO: Chihuahua: Chihuahua, *Pringle 800* (F, C); Santa Eulalia Mts., *Pringle 51* (F). Coahuila: Sierra Mojada, *Jones in 1892* (P); Saltillo, *Palmer 91 in 1898* (C, F), *295 in 1902* (F). Tamaulipas: Jaumave, *Rozynski 454* (F). San Luis Potosi: Minas de San Rafael, *Purpus 5469* (F, C, G).

The collection from San Luis Potosi has the leaves arranged in strikingly opposite and discrete pairs rather than congested or turned at various angles but I have observed this same peculiarity in one plant of *Euphorbia albomarginata* T. & G., La Verne, Calif., *Wheeler 2580* (W). In this latter case the atypical plant was sterile and the surrounding fertile plants were typical. This character seems to be of no consequence.

I had intended (Bull. So. Cal. Acad. Sci. 33: 106. 1934) to reduce this species to a variety of another species. Further consideration, however, has led me to keep it as a species.

The specimen of this species mentioned as *Euphorbia melanadenia* Torr. var. *subinappendiculata* Engelm. ex Boiss. by Boissier, DC. Prod. **15**^{2}**:** 32. 1862, collected by Gregg at "Monterey Californiae" must have come from Monterey, Nuevo Leon, Mexico, for *E. cinerascens* does not occur in California and Gregg is known to have collected near Monterey, Mexico, as evidenced by the collection of *Oenothera Greggii* Gray var. *Pringlei* Munz, Saltillo, Coahuila, *Gregg 33*, cited by Munz, Am. Jour. Bot. **16:** 711. 1929.

In a list of manuscripts and herbarium names taken up by Boissier in De Candolle's Prodromus, **15**^{2}. 1896, appended to Engelmann's article, "On the Euphorbiaceae in Candolle's Prodromus," by the editors Trelease & Gray on page 445 of "Botanical Works of the late Geo. Engelmann" appears "*E. melanadenia* var. *subappendiculata*." This spelling of the varietal name differs from the "*subinappendiculata*" published by Boissier.

20. EUPHORBIA VALLIS-MORTAE (Millsp.) J. T. Howell, Madroño **2:** 19. 1931. *Chamaesyce vallis-mortae* Millsp., Field Mus. Pub. Bot. 2: 403. 1916.

Perennial, usually forming a dense rounded plant up to 15 cm. high; herbage hoary-tomentose throughout; stems usually arising from 2–4 cm. below the surface of the ground, this portion brown and glabrous, aërial portion to 1 mm. diam., internodes mostly 1–2.5 cm. long; but much shortened toward the tip thereby congesting the leaves and involucres; leaf blades suborbicular to oblong-ovate, mostly 4–8 mm. long; lower stipules united,

filiform, ca. 1 mm. long, densely hairy, upper stipules distinct, filiform, ca. 0.7 mm. long, densely hairy; peduncles stout, to 1.5 mm. long, densely hairy; involucres solitary in the axils, campanulate, ca. 2 mm. diam., densely hairy without, with long erect hairs extending halfway down within opposite glands; lobes with long ascending hairs within, equaling or slightly exceeding the glands, deltoid, entire; glands yellowish or reddish, transversely oblong, to 1 mm. long, the distal slightly shorter; appendages white, as wide as and a little longer than the glands, entire or crenulate, with numerous short hairs beneath and on the margins and a few above; fifth gland absent; sinus U-shaped, with long erect hairs at the bottom; bracteoles mostly united into one group opposite each gland, of 6–10 bracteoles, more or less united below, adnate to the involucre, sometimes with shorter bracteoles outside the androped fascicle, all hairy above; andropeds 3–5 per fascicle, 17–22 per involucre, ca. 2 mm. long, slightly exserted, sometimes with a few short hairs above; gynoped densely hairy, long-exserted and reflexed at maturity; ovary three-lobed, densely hairy; styles ca. 0.5 mm. long, parted to the middle, short-hairy below; capsule tomentose, three-angled, 2 mm. long and diam.; seeds quadrangular, ca. 1.5 mm. long, ca. 0.75 mm. tangentially and radially, ovate radially, raphe straight, back rounded in tangential silhouette, base obtusely truncate, coat white, microreticulate.

Type locality: between Mohave and Keeler northwestern Mohave Desert, Calif., not Death Valley as stated by Millspaugh. Distribution: northwest Mohave Desert north to Owens Lake, California. Specimens seen: Co.?: Between Mohave & Keeler, *Coville & Funston 1008* (F, fragment of type). Inyo Co.: west shore Owens Lake, *Hall & Chandler 7323* (P, C). Kern Co.: Indian Wells, *Hoffmann 617* (P); 6 mi. N Freeman, *Hoffmann 585* (CA, SB); Red Rock Canyon, *Peirson 7335* (P, Peir), *Howell 4973* (Peir, CA); Dove Springs, *Hoffmann in 1931* (SB).

21. EUPHORBIA PEDICULIFERA Engelm. in Torr., Bot. Mex. Bound. Surv., 186. 1859. *Chamaesyce pediculifera* (Engelm.) Rose & Standley, Contr. U. S. Nat. Herb. 16: 12. 1912.

Perennial from a taproot stout in age; stems prostrate to erect, appressed pubescent, glabrate in age, up to 2 mm. in diam. toward the base, internodes up to 5 cm. long, often very short toward the stem tips thus congesting the involucres; leaves closely appressed pubescent to subglabrous, blades 2–30 mm. long, 1–10 mm. wide, ovate with oblique base, oblong with subsymmetrical base to spathulate and even narrowly linear with symmetrical base, petioles 1–2 mm. long, amplexicaul on ventral side of stem; stipules mostly less than 0.5 mm. long, the ventral united, the upper distinct; peduncles clothed as the leaves, up to 1.5 mm. long; involucres campanulate, 1.5–2 mm. long, solitary in the axils, sometimes congested at the branch tips by shortening of the terminal internodes but not strictly glomerulate, closely appressed

pubescent to sub-glabrous without, more or less short hairy within above; lobes deltoid, hairy, equaling the glands; glands transversely oblong, 0.5 mm. wide, 0.75–1.25 mm. long, dark red-purple; appendages absent or up to 2 mm. wide and 3 mm. long, entire or slightly lobed, glabrous; fifth gland very short or usually absent; sinus U-shaped, hairy, little depressed; bracteoles shorter than the andropeds, usually very hairy above, in one group of 6–8 opposite each gland, united at the base and adnate to the involucre; andropeds ca. 1.25 mm. long, included or shortly exserted, glabrous or with few hairs above, 4–5 per fascicle, 22–25 per involucre; gynoped nearly glabrous or hairy nearly throughout, exserted and reflexed at maturity; ovary very slightly lobed, densely hairy, tapering upward, styles ca. 1 mm. long, slender, parted to the base, short hairy on the lower side to the tip; capsule appressed pubescent, widest below the middle, 2 mm. in diam. and long, markedly three-lobed, the lobes obtuse, axis persistent; seeds cylindrical, 1–1.3 mm. long, 0.6–0.7 mm. diam. encircled by 4 or 5 rounded ridges with V-shaped channels between, coat white.

KEY TO VARIETIES

Leaves ovate to lanceolate with obtuse apex; bracteoles 6–8, united only at base and conspicuous.....21a. var. *typica*

Leaves strictly linear; bracteoles reduced, usually inconspicuous, if conspicuous, united upward.....21b. var. *linearifolia*

21a. **Euphorbia pediculifera** Engelm. var. **typica** Wheeler nom. n. *Euphorbia involuta* Millsp., Proc. Calif. Acad. Sci. II **2**: 227. 1889. *Chamaesyce involuta* Millsp., Field Mus. Pub. Bot. 2: 410. 1916. *Euphorbia pediculifera* Engelm. var. *involuta* (Millsp.) Johnston, Proc. Calif. Acad. Sci. IV **12**: 1070. 1924. *Euphorbia conjuncta* Millsp., Proc. Calif. Acad. Sci. II **2**: 227. 1889. *Chamaesyce conjuncta* Millsp. Field Mus. Pub. Bot. 2: 408. 1916. *Euphorbia pediculifera* Engelm. var. *inornata* T. S. Brandegee, Zoe **5**: 209. 1905. E. vermiformis Jones, Con. West. Bot. 16: 23. 1930.

Type locality: Sonora, Mexico. Distribution: southeastern California, Arizona, Lower California, Sonora, Sinaloa. Representative specimens seen: CALIFORNIA: Imperial Co.: Carrizo (Cariso) Mt., *T. S. Brandegee in 1905* (C); Midway Well, *Peirson 9796* (Peir, W); 20 mi. NE Ogilby, *Munz & Hitchcock 12155* (P). ARIZONA: Coconino Co.: Williams Fork, *Palmer 515 in 1876* (G). Yavapai Co.: Congress (C. Junction), *Jones in 1903* (D, P), *Orcutt in 1896* (C). Yuma Co.: Ehrenberg, *Palmer in 1876* (G). Maricopa Co.: Maricopa Mts. (Hills), *Pringle in 1882* (G); Gila Bend, *Harrison & Kearney 7896* (P, F). Pinal Co.: Mammoth, *Harrison & Kearney 6692* (P). Pima Co.: Hartts Ranch, *Thornber 122* (P, C); Gunsight Peak, *Fosberg 7434* (UCLA); Ajo, *Jones 24858* (C, P, G, CA in part), *Jones 24856* (P, type of *E. vermiformis*). Santa Cruz Co.: Nogales, *Peebles, Harrison & Kearney 4599* (UCLA, P), *5576* (UCLA), *8151* (CA). Cochise

Co.: Chiricahua Mts., Bowie (Fort B.), *Lemmon 283* (C, G). LOWER CALIFORNIA: West Coast, *Com. Evers of "Narragansett" in 1873*(G); Big Canyon, Tantillas Mts. 34 mi. from Tecate, *Palmer 453 in 1875* (F, G); Santa Rosalia, *Jones 22619* (P); Purisima, *T. S. Brandegee in 1889* (G, C, isotypes of *Euphorbia conjuncta* Millsp.); Comondu, *T. S. Brandegee in 1889* (C, isotype of *Euphorbia involuta* Millsp.); Los Angeles Bay, *Palmer 631 in 1887* (G); Espiritu Santo Island, *Johnston 3991a* (C, CA, G), *Craig 656* (P); La Paz, *Palmer A in 1890* (C, G), *Jones 24501* (P, UCLA). SONORA: No locality, *Schott, no date or no.* (G); Poso Verde, *Schott III 12 in 1855* (F); 15 mi. N Magdalena, *Fosberg 7430* (P, UCLA); Pitiquito, *Pringle in 1884* (G, F); Hermosillo, *Jones 22615* (G, P). SINALOA: Confradia, *T. S. Brandegee in 1904* (F, G, C type of *Euphorbia pediculifera* Engelm. var. *inornata* T. S. Brandegee); Topolobampo, *Palmer 212 in 1897* (G), *Rose, Standley & Russell 13276* (F); San Blas, *Jones 23324* (P).

Included in this variety is a great diversity of habit and leaf shape. It appears to me that the leaf shape varies more according to the situation in which the plant is growing than according to any innate tendency.

21b. EUPHORBIA PEDICULIFERA Engelm. var. LINEARIFOLIA Wats., Proc. Am. Acad. **24**: 76. 1889.

Type locality: High Mts., Guaymas, Sonora, Mexico. Distribution: Guaymas and San Pedro Bay, Sonora. Specimens seen: SONORA: Guaymas, *Palmer 627 in 1887* (F, G, C), *Palmer 215 in 1887* (C, G type), *T. S. Brandegee in 1893* (C); San Pedro Bay, *Craig 671* (P).

22. EUPHORBIA FENDLERI Torr. & Gray, Pacif. Rail Rep. II 2: 175. 1855. *Anisophyllum Fendleri* (T. & G.) Klotzsch & Garcke, Abh. Akad. Berl., 1859 (1860) 26. *Chamaesyce Fendleri* (T. & G.) Small, Fl. SE U. S., 710. 1903. *Euphorbia rupicola* Scheele, Linnaea **22**: 153. 1849, not Boissier.

Glabrous perennial from a taproot woody in age; stems several to numerous from the base, decumbent to erect, up to 15 cm. long, slender, internodes up to 2 cm. long; leaf blades entire, ovate-orbicular with oblique base to lanceolate, petioles mostly ca. 1 mm. long; stipules up to 1 mm. long, distinct, narrowly linear, mostly entire, rarely with a few hairs; peduncles up to 4 mm. long, glabrous; involucres solitary in the axils, glabrous, 1.25–1.75 mm. diam., campanulate to turbinate, glabrous without, with short hairs within above opposite the glands, lobes deltoid-shortly-attenuate, hairy within below, equaling the glands; glands reddish, 1.5–4 times as long as wide, concave or convex, up to 1 mm. wide; appendages white, glabrous, 0.5–1 mm. long, as wide as the gland at least at the base, obtuse-crenate to entire and narrowly deltoid, or parted into 2–4 narrow ligules; fifth gland shorter than the lobes, linear; sinus very broad and little depressed; bracteoles forming a single appendage adnate below to the involucre opposite each gland, 3–5 parted and

hairy above; andropeds 1.25 mm. long, glabrous, 5–7 per fascicle, 25–35 per involucre; gynoped glabrous, exserted and reflexed at maturity; ovary glabrous, three-lobed; styles glabrous, ca. 0.4 mm. long, bifid to the middle, curved upward, thickened at the base; capsule glabrous, spheroid, three-angled, ca. 2.25–2.5 mm. long, axis persistent; seeds quadrangular, 2–2.25 mm. long, ca. 1 mm. radially, 1–1.2 mm. tangentially, ovate-acute radially, angles prominent, front facets concave, mostly smooth, back facets slightly wrinkled, coat white, microreticulate.

KEY TO VARIETIES

Plants decumbent to erect; leaves ovate-orbicular to ovate-lanceolate; appendages obtuse, crenate ..... 22a. var. *typica*

Plants erect and leaves lanceolate.

Appendages narrowly deltoid, entire ..... 22b. var. *chaetocalyx*

Appendages parted into 3–4 narrowly linear segments; root very thick ..... 22c. var. *triligulata*

22a. **Euphorbia Fendleri** T. & G. var. **typica** Wheeler n. nom. *E. rupicola* Scheele. Linnaea **22:** 153. 1849, not Boissier. *E. Fendleri* T. & G. var. *dissimilis* Payson, Bot. Gaz. **6:** 379. 1915. *Chamaesyce Gooddingii* Millsp., Field Mus. Pub. Bot. 2: 406. 1916.

Type locality: "Big Springs of the Colorado, New Mexico." Probably somewhere near Sante Fe, New Mexico, fide Standley Contr. U.S. Nat. Herb. 13: 199. 1910. Distribution: California north to Utah, east to Kansas, and south to Sonora, Mex. Representative specimens seen: CALIFORNIA: Co.?: Desert Wells, Southeastern Calif., *Purpus 5689 in part* (C). San Bernardino Co.: Clark Mt. E Mohave Desert, *Jaeger in 1930* (P). Inyo Co.: Westgard Pass, White Mts., *Duran 547*, (P, C, D, CA, RS). NEVADA: Clark Co.: Charleston Mts.: Lee Canyon, *Heller 11058* (G, C, F type of *Chamaesyce Gooddingii* Millsp.); Kyle Canyon, *Jaeger in 1926* (P, CA). Lincoln Co.: Caliente, *Jones in 1904* (P). Esmeralda Co.: Candelaria, *Shockley 312* (C, D in part). UTAH: Duchesne Co.: Myton, *Jones in 1908* (P). Carbon Co.: Price, *Stokes in 1898* (C), *in 1900* (D), *Flowers 6390* (F). Grand Co.: Thompson's Springs, *Jones in 1891* (P). Beaver Co.: Frisco, *Jones in 1880* (P); Milford, *Jones in 1880* (P). Garfield Co.: Tropic, *Jones in 1894* (P). ARIZONA: Mohave Co.: Peach Springs, *Wilson in 1893* (C). Coconino Co.: Flagstaff, *Jones 336* (P). Yavapai Co.: Skull Valley, *Jones in 1903* (P). WYOMING: Laramie Co.: Hartville, *Nelson 8326* (P). COLORADO: Yuma Co.: Wray, *Eggleston 15201* (F). Montrose Co.: Naturita, *Payson 119*, fragment of type of *Euphorbia Fendleri* var. *dissimilis* (W); Paradox, *Walker 110* (P, D). Gunnison Co.: Barnum, *Eastwood in 1910* (C, CA). Fremont Co.: Canyon City, *T. S. Brandegee 866* (C), *Johnston & Hedgecock 739* (C). NEW MEXICO: Santa Fe Co.: Canoncito,

Heller 3727 (D); Big Springs of the Colorado, *Fendler 800*, type collection of *E. Fendleri* var. *typica*, (F). San Juan Co.: Farmington, *Osterhout 6948* (P); Aztec, *Baker 613* (P). Chaves Co.: 20 mi. S Rosswell, *F. S. & E. S. Earle 313* (P). KANSAS: Trego Co.: no loc., date, or no., *Bodin* (F). Morton Co.: Richfield, *Thompson 167* (G). OKLAHOMA: Ellis Co.: Shattuck, *Stevens 2944* (D). Beaver Co.: Knowles, *Stevens 338½* (P). TEXAS: Kendall Co.: Baerne, *Palmer 9912* (D). Reeves Co.: Pecos, *Gillespie 5262* (D). Brewster Co.: Chisos Mts., *Ferris & Duncan 2920* (D). Randall Co.: Canyon, *Benke 4987* (F). Erath Co.: Dublin, *Maxwell 52* (F). Hood Co.: Granbury, *Reverchon in 1877* (F). Kerr Co.: Kerrville, *Heller 1870* (C). Travis Co.: Austin, *Hall 545 in 1872* (F, P). Comal Co.: "Comanche Springs, New Braunfels, etc.," *Lindheimer 1138*, type collection of *E. rupicola* Scheele, (C), *1137* (C). Bexar Co.: Leon Springs, *Clemens 425* (P).

The extreme forms of variety *typica* and *chaetocalyx* are readily distinguishable by the habit, leaf shape and appendages, but a complete series of intergrades exists. The following specimens are intergrades between var. *typica* and *chaetocalyx*: ARIZONA: Co.?: Between Jacob's Station and Houserock, Kaibab, *Jaeger in 1927* (P). NEW MEXICO: Co.?: San Ysidro, *Arsène 19052* (P), *19053* (F), *Arsène & Benedict 17541* (F). Bernalillo Co.: Albuquerque, *Jones in 1880* (P). Sierra Co.: Kingston, *Metcalfe 1488* (P, CA, F). TEXAS: Co.?: Indian Hot Springs, *Jones 25996* (P).

22b. EUPHORBIA FENDLERI T. & G. var. CHAETOCALYX Boissier DC. Prod. **15**[2]: 39. 1862. *Chamaesyce chaetocalyx* (Boiss.) Wooton & Standley, Contr. U. S. Nat. Herb. 16: 144. 1913.

Type locality: New Mexico. Distribution: Arizona, New Mexico, and Western Texas. Representative specimens seen: ARIZONA: Mohave Co.: Peach Springs, *Greene in 1889* (F), *Wilson in 1893* (C). Coconino Co.: Cameron, *Hanson A212* (F). Navajo Co.: no loc., *Toumey in 1896* (F). NEW MEXICO: Co.?: no loc., *Wright 1847* (F, fragment of type from herb. Boissier). Socorro Co.: Socorro, *Eggleston 16238* (F). Doña Ana Co.: Conkling Cave, Pyramid Peak Range, *Fosberg S3245* (P). Otero Co.: High rolls, Lincoln Forest, *Eggleston 14407* (G). TEXAS: El Paso Co.: El Paso, *Jones 4217* (P). Culberson Co.: McKittrick Canyon, Guadalupe Mts., *Moore & Steyermark 3532* (C, CA). Brewster Co.: Chisos Mts. *Mueller 8074* (F).

22c. **Euphorbia Fendleri** T. & G. var. **triligulata** Wheeler n. var.

Radix multum crassa; caulibus erectis; foliis lanceolatis; appendiculis in 3–4 anguste linearibus segmentis partitis.

Type locality: Boquillas Canyon above Boquillas, Brewster Co., Texas. Known only from the type locality. Specimens seen: TEXAS: Boquillas Canyon above Boquillas, Brewster Co.; *Moore & Steyermark 3444 in 1931* (G, type; CA, D, isotypes).

23. EUPHORBIA ALBOMARGINATA Torr. & Gray, Pacif. Rail. Rep. 2: 174. 1855. *Chamaesyce albomarginata* (T. & G.) Small, Fl. SE U. S., 710. 1903. *Euphorbia stipulacea* Engelm. ex Boissier, (in synonomy), DC. Prod. 15[2]: 30. 1862.

Glabrous prostrate perennial from a taproot woody in age; stems several to numerous, up to 30 cm. long, internodes up to 6 cm. long but usually much shorter, nodes often rooting; leaf blades mostly 3–6 mm. long, sometimes as much as 15 mm. long, orbicular to oblong, sometimes with a red spot in the middle on the upper surface, midrib usually not prominent, lateral veins rarely evident, margin entire, petioles 0.5–1 mm. long; both upper and lower stipules united into a glabrous, white, membranous, deltoid to subulate, usually lacerate-margined scale; peduncles slender, glabrous, mostly 2–4 mm. long; involucres solitary in the axils, 1.5–2 mm. diam., open-campanulate to turbinate, glabrous without and within; lobes short-hairy within below, exceeding the glands, narrowly deltoid-attenuate; glands 0.5–1 mm. long, transversely oblong, concave, ochroleucous or mostly maroon; appendages usually conspicuous, wider and longer than the glands, white, glabrous, entire or slightly crenate; fifth gland linear, equaling the lobes, hairy within below; sinus U-shaped, little depressed; bracteoles forming one conspicuous, upwardly expanded, mostly 2–4 divided, hairy radial appendage two-thirds as long, to as long as, the andropeds, adnate below to the involucre opposite each gland; andropeds 1–1.3 mm. long, glabrous, 3–6 per fascicle, 15–30 per involucre; gynoped glabrous, long-exserted and mostly reflexed at maturity; ovary glabrous, three-lobed, styles bifid to below the middle, ca. 0.5 mm. long, glabrous, clavate, spreading-erect; capsule sharply three-angled, glabrous, ovoid, ca. 1.75 mm. long; seeds 1.3–1.4 mm. long, ca. 0.6 mm. radially and tangentially, quadrangular, narrowly oblong radially, base obtuse or truncate, facets concave or convex, smooth, angles mostly rounded, coat microreticulate in definite lines, opaque-white or so thin as to little obscure the brown testa; capsule axis persistent.

Type locality: Not stated. Distribution: California, northeast to Utah, southeast to Texas and Sonora. Representative specimens seen: CALIFORNIA: Inyo Co.: Surprise Canyon, Panamint Mts., *Ferris 7951* (P, D), *Howell 4040* (CA); Shepherd's Canyon, Argus Mts., *Coville & Funston 735* (D); Emigrant Springs, *Parish 10086* (F, C). Kern Co.: Canyon W Cuddy Canyon, Mt. Piños Region, *Munz 7061a* (P); Ft. Tejon, *Abrams & McGregor 284* (D). Los Angeles Co.: Lancaster, *Elmer 3630* (CA, P, C); Inglewood, *Abrams 2480* (P, C, D). San Bernardino Co.: Mohave Desert:

7 mi. S Barstow, *Johnston 6498* (P); Cactus Flat, San Bernardino Mts., *Munz 10511* (P); Redlands, *Budd in 1901* (P, D). Riverside Co.: Corona, *Munz & Harwood 3247* (P); Whitewater, *Vasey 443* (F). San Diego Co.: San Felipe, *Jones in 1906* (P). Imperial Co.: Durmid, *Parish 8066* (D). NEVADA: Clark Co.: Colorado River bottoms 15 mi. E Searchlight, *Parish 10290* (F, C). Lincoln Co.: Caliente, *Jones in 1904* (P). UTAH: Washington Co.: St. George, *Jones 1663* (P, CA). ARIZONA: Mohave Co.: Hackberry, *Jones in 1903* (P). Coconino Co.: Grand Canyon of the Colorado, *Millspaugh 149* (F). Yavapai Co.: Humboldt, *Peebles & Harrison 4117* (UCLA). Maricopa Co.: Aguila, *Jones 26002* (P); Phoenix, *Jones in 1903* (P). Pinal Co.: Superior, *Peebles, Harrison & Kearney 5076* (UCLA). Pima Co.: Babiroquivra Mts., *Jones 24852* (UCLA, C, CA, P). NEW MEXICO: Grant Co.: Cliff, *Eggleston 19990* (F). Sierra Co.: Kingston, *Metcalfe 1101* (P, CA, F). Luna Co.: Deming, *Jones 3802* (P, CA). Doña Ana Co.: south end Organ Mts., *Fosberg S3212* (P). Lincoln Co.: Gray, *Skehan 8* (P, F, C). Chaves Co.: 20 mi. S Roswell, *S. F. & E. F. Earle 309* (P). TEXAS: Presidio Co.: Presidio, *Harvard, no date or no.* (F). Brewster Co.: banks of Rio Grande, Boquillas Canyon, *Moore & Steyermark 3432* (CA). Bexar Co.: San Antonio, *Sculy 2160* (P). Webb Co.: Laredo, *Palmer 11274* (C). OKLAHOMA: Harmon Co.: Hollis, *Stevens 1105* (G, D). BAJA CALIFORNIA: 50 mi. SE Tecate, *Munz 9553* (P). SONORA: 15 mi. N Magdalena, *Fosberg 7429* (UCLA, D, P); Hermosillo, *Rose, Standley & Russell 12446* (F). Guaymas, *Palmer 93 in 1887* (C). CHIHUAHUA: Casas Grandes, *Goldman 406* (F, G); Chihuahua, *Palmer 371 in 1908* (F). SINALOA: Culiacan, *T. S. Brandegee in 1904* (F, C), *Rose, Standley & Russell 14931* (F, G), *Goldman 372* (F, G). COAHUILA: Sabinas, *Nelson 6792* (F). DURANGO: Durango, *Palmer 296 in 1896* (F, C); Santiago Papasquiaro, *Palmer 42 in 1896* (F, C).

In the California plants the white seed coat is very thick. In most of the plants from elsewhere this coat is very thin so that the seeds appear brownish. Some plants in Arizona, as Babiroquivra Mts. *Jones 24852* have large, obtuse, and veiny leaves. The following local peculiarities are noted from California: San Bernardino Co.: Fimbriate beneath the capsule, Cactus Flat; stipules adnate to petioles, 7 mi. S Barstow. Inyo Co.: Surprise Canyon, Panamint Mts., *Ferris*, stipules distinct but membranous.

Occasionally the leaves have a red maculation in the center. There is an apparently unpublished herbarium name based on this character.

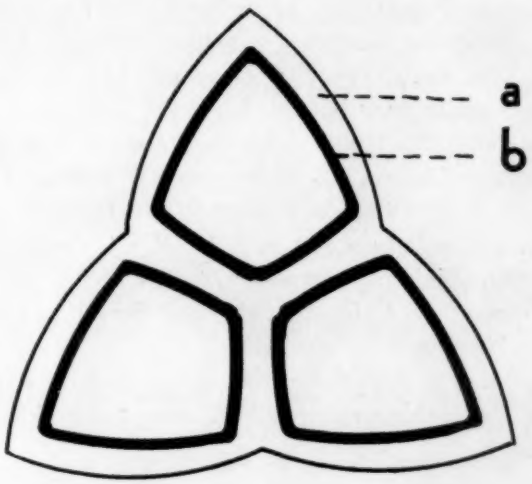
24. EUPHORBIA SERPENS H. B. K., Nov. Gen. et Sp. 2: 52. 1817, not Baill., or Balb. ex Boiss. *Anisophyllum serpens* (H. B. K.) Klotzsch & Garcke,

Phys. Abh. Akad. Wiss. Berlin, 1859 (1860) 23. *Chamaesyce serpens* (H.B.K.) Small, Fl. SE U. S., 709. 1903. *Euphorbia serpens* H.B.K. *A. genuina* Thellung, in Aschers. & Graebn., Syn. Flora Mittel. **7:** 442. 1916. *E. serpens* H.B.K. var. *imbricata* Boiss., DC. Prod. **15²:** 30. 1862. *E. serpens* H.B.K. *A. genuina* Thellung II *imbricata* (Boiss.) Aschers & Graebn., Syn. Flora Mittel. **7:** 442. 1916. *E. serpens* H.B.K. var. *radicans* Engelm. ex Boiss., DC. Prod. **15²:** 30. 1862. *E. radicans* Moric [in Berland pl. exs.], nach Klotzsch & Garcke, Phys. Abh. Akad. Wiss. Berlin, 1859. 24 (1860), (as a synonym of *Anisophyllum serpens*). *E. Engelmannii* Sennen var. *radicans* (Moric) Sennen & Pau, in Sennen pl. d.'Esp. n. 1442, Bull. Geogr. bot. 23ᵉ annee [Ser. 4ᵉ] Nr. 295/7. 230. 1914. *Chamaesyce radicans* (Moric) Millsp., Field Mus. Pub. Bot. 2: 411. 1916. *Euphorbia herniaroides* Nutt., Pl. Arkans., 171. 1837. *E. flexicaulis* Scheele, Linnaea **22:** 154. 1849. *E. serpens* H.B.K. *A. genuina* Thellung III *flexicaulis* (Scheele) Thellung in Aschers. & Graebn. Syn. Fl. Mittel. **7:** 442. 1916.

Prostrate annual, often very leafy, herbage glabrous throughout; stems slender, up to 30 cm. long, internodes to 3 cm. long, nodes sometimes rooting; leaf blades 2–7 mm. long, ovate-orbicular to oblong, base oblique except in the smallest, margin entire, petioles mostly less than 1 mm. long; both upper and lower stipules united into a white, membranous, glabrous scale less than 1 mm. long with more or less lacerate margin; peduncles up to 2 mm. long, expanding upward, glabrous; involucres solitary in the axils, turbinate, 1 mm. long, 1 mm. diam., tapering to the thick upper end of the peduncle, glabrous without and within; lobes deltoid, sometimes with a few hairs on the margins below, apex acute to attenuate, equaling or slightly exceeding the glands; glands transversely oblong, ca. 0.2 mm. long, ochroleucous, concave; appendages mostly present, little wider than the glands, white, glabrous, margin mostly crenate; fifth gland linear, exceeding the glands, with a few marginal hairs at the base; sinus slightly depressed; bracteoles forming a single, linear or broader, entire or parted, slightly hairy appendage 0.6 mm. long or shorter, adnate below to the involucre opposite each gland; andropeds 5 per involucre, glabrous, 1 mm. long, equaling the glands; gynoped glabrous, exserted and mostly reflexed at maturity; ovary 3-lobed, glabrous, styles glabrous, markedly clavate, 0.2 mm. long, usually parted to below the middle, rotately spreading; capsule glabrous, 3-angled, ca. 1.2 mm. long; seeds ovoid with rounded angles or somewhat turgid-quadrangular with more prominent angles, ca. 1 mm. long, ca. 0.5 mm. radially and tangentially, coat microreticulate, white, with the brown testa showing through; capsule axis persistent.

Type locality: Cumana, Venezuela. Distribution: Illinois, Iowa, Kansas, and Colorado southward through Mexico to South America. Representative specimens seen: NEW MEXICO: Doña Ana Co.: Mesquite, *Fosberg S3615* (P, C). Eddy Co.: Carlsbad, *Tracy 8170* (F). Weld Co.: New Windsor, *Osterhout in 1899* (P, F). Fremont Co.: Canyon City, *T. S.*

Brandegee in 1873 (C). NORTH DAKOTA: Barnes Co.: Kathryn, *Bexgmen 971* (F). KANSAS: McPherson Co.: Lindsborg, *Bodin in 1884* (F). Hamilton Co.: Syracuse, *Thompson 136* (C). OKLAHOMA: Ottawa Co.: Miami, *Stevens 2305* (P). TEXAS: Dallas Co.: Dallas, *Reverchon in 1879* (F). Travis Co.: Austin, *Hall in 1872* (P, F). Hayes Co.: San Marcos, *Palmer*



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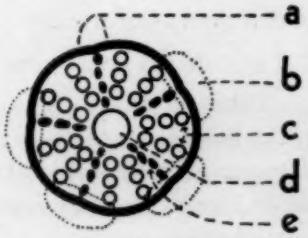

3

Explanatory diagrams of the reproductive structures of Euphorbia, sect. Anisophyllum

Fig. 1. Diagrammatic transverse section of capsule. a. Carpel wall. b. Seed testa.

Fig. 2. Diagram of involucre spread open. a. 5th gland. b. Sinus. c. Gland. d. Involucral lobe.

Fig. 3. Diagrammatic transverse section of involucre cut just below the intervals between the glands and the lobes. a. Interval of reduced 5th gland. b. Silhouette of gland to show its relative position. c. Andropeds. d. Gynoped. e. Bracteole.

12095 (C). Comal Co.: New Braunfels, *Lindheimer 693*, type collection of *Euphorbia serpens* var. *imbricata* Boiss., (F). Bexar Co.: San Antonio, *Bebb 2364* (F), *Clemens 421* (P), *Jermy 130* (G). Gonzales Co.: No loc., *Bogusch 936* (F). Nueces Co.: Corpus Christi Bay, *Heller 1467* (P, C, UCLA). Brazoria Co.: Columbia, *Palmer 6679* (F). Starr Co.: Rio Grande City, *Neally in 1889* (F). MISSOURI: Jefferson Co.: St. Louis, *Glatfelter in 1894* (F). ARKANSAS: Pulaski Co.: Little Rock, *Hasse in 1886*. TENNESSEE: Davidson Co.: Nashville, *Gattinger* (*Curtiss*) *2500* (F). LOUISIANA: Plaquemines Co.: Port Eads, *Tracy & Lloyd 210* (F). FLORIDA: Escambia Co.: Pensacola, *Curtiss 5920* (C, D). LOWER CALIFORNIA: Comondu, *T. S. Brandegee in 1889* (F). SONORA: Lerdo, *Palmer 954 in 1889* (F). COAHUILA: San Lorenzo Laguna, 22–27 leagues SW Parras, *Palmer 1192 in 1880* (F). TAMAULIPAS: Tampico, *Palmer 521 in 1910* (F, CA). SAN LUIS POTOSI: San Dieguito, *Palmer 121 in 1910* (F, C). GUATEMALA: Department of Retahulen: Mulua, *Kellerman 5173* (F).

The plant from Lower California, although far out of range, is typical. There may have been an error in labeling.

I have not seen type material of this species and consequently the entity here called *Euphorbia serpens* H.B.K. may not be identical with the Venezuelan plant.

EXCLUDED OR DOUBTFUL SPECIES

1. EUPHORBIA CAPITELLATA Engelm. ex. Torrey, Bot. Mex. Bound. Surv. II **2**: 188. 1859. See Bull. Torrey Club **62**: 537. 1935 for synonymy.

This species is sometimes entire-leaved and might be thought to belong in this group but usually at least a few of the leaves are serrate.

2. CHAMAESYCE TAMAULIPASANA Millsp., Field Mus. Pub. Bot. 2: 403. 1916.

Although described as entire-leaved by Millspaugh the type has many of the leaves definitely serrate which character excludes it from this group if geographical considerations do not. Although this species is valid as far as I know I refrain from making a new combination of it until I study related species.

GRAY HERBARIUM,
HARVARD UNIVERSITY,
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The structure of the growing point and the development of the bud scales of Morus alba[1]

G. L. Cross

(WITH SIXTEEN TEXT-FIGURES)

In most text books of botany bud scales are described as transformed or modified foliage leaves. The general applicability of this interpretation seems uncertain on the grounds of insufficient knowledge. Recent researches indicate that very little is known about the developmental mechanics of foliar structures other than foliage leaves. As far as the writer has been able to discover, Foster (1935) has provided the only complete histogenetic study of a bud scale to be found in the literature. Since the time of Grew numerous observations of the gross structure of scales have been made, and histological studies of mature tissues have occasionally appeared. A confusing array of interpretations based on such researches is presented to one who would review the literature, although Foster (1928) has provided a very helpful résumé to which students of foliar structures are referred.

Botanists differ concerning the value of ontogeny as a criterion of relationship, and admittedly, such evidence should be used with caution in making phylogenetic interpretations. When attempting to find the morphological category to which the organs of a given plant belong, however, it is necessary to determine all basic points of similarity and difference. Such definite information can be accumulated by studying the organs completely, i.e. throughout their ontogenetic processes, and will naturally involve a consideration of the origin and development of their primordia. Any morphological conclusions based on less complete information are apt to be inaccurate and misleading.

Although the morphological interpretation of bud scales has always been somewhat in doubt, the "transformation theory" supported by Goebel (1928) gradually became prominent during the first quarter of the twentieth century. Goebel developed the view that all foliar primordia are potential foliage leaves. When a bud scale is produced an "arrest" occurs in the development of a foliage leaf primordium after which this structure, by divergent development, becomes a scale. He based his conclusions upon morphological and experimental data which have been discussed by Foster (1928).

Recently the views of Goebel have been challenged by Foster, who has reattacked the problem from an ontogenetic viewpoint, and in a series of papers has presented evidence that foliage leaf and bud scale primordia

[1] Contribution from the Botanical Laboratory, University of Oklahoma, 40.

are quite distinct at a very early state—that there is neither arrest nor transformation during the ontogeny of the bud scale. In a recent paper Foster (1935) contributes information and evidence concerning the structure of the growing point, initiation of foliar primordia, comparative histogenesis and tissue specialization in the foliage leaves and bud scales of *Carya Buckleyi* var. *arkansana*. The present writer has nearly completed a similar study involving the bud scales, foliage leaves and stipules of the genus *Morus*, but unusual features concerning the bud scale have been found which seem to justify a preliminary description.

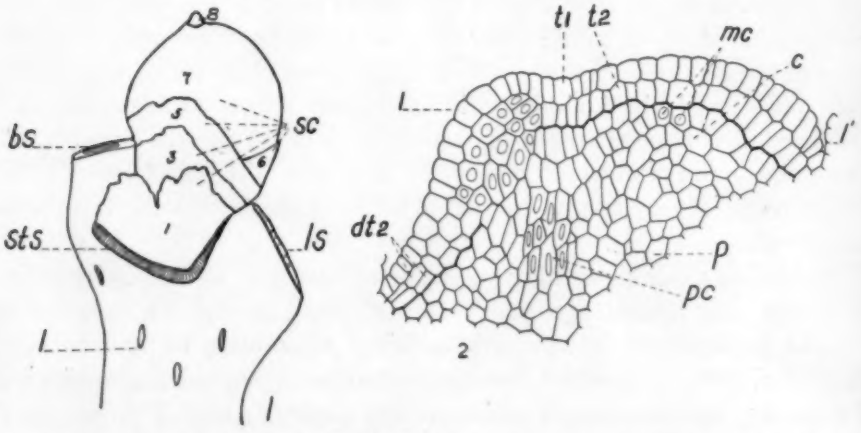


Fig. 1. Winter bud of portion of twig of *Morus alba; l*, lenticel; *sts*, stipule scar; *ls*, leaf scar; *bs*, terminal bud scar; *sc*, bud scales. ×8.

Fig. 2. Median longitudinal section through stem tip and young leaf; *pc*, procambial tissue that will become the median leaf trace of the young leaf to the left; *p*, pith; *dt2*, cells derived from T-2, contributing to cortex of internode; *l*, foliage leaf initial; *t1*, outer tunica; *t2*, inner tunica; *mc*, initial cells of corpus; *c*, corpus; l^1, older foliage leaf.

The histogenesis of the bud scale of *Morus alba* L. has been found to differ radically from Foster's account of scale development in *Carya Buckleyi* var. *arkansana*. The differences are of a fundamental nature and suggest the need of further researches involving additional genera. The present account is purely descriptive. No interpretations are made as it is intended for these to appear later in a paper dealing with comparative histogenesis of foliar structures in the genus.

THE SHOOT SYSTEM

The twigs of *Morus alba* are slender and cylindrical. At the base occur the narrow scars of from eight to eleven two-ranked bud scales. The leaf

scars occur in two opposite rows. Normally five or six of the latter appear, but this number may be greatly increased, especially in the case of coppice shoots.

The leaf scars are round, and are raised somewhat above the surface of the twig. The bundle traces, from eight to eleven in number, are scattered near the center of the scar. They protrude definitely above the surface of the scar. The stipule scars occur laterally at the level of the median portion of the leaf scar (fig. 1).

Axillary buds are present, all of which contain flowers. One or two smaller, accessory collateral buds usually accompany the main lateral bud. Terminal resting buds do not form. The apical meristem, with several young leaves in various stages of development, degenerates and usually drops from the twig at the end of the period of bud expansion in the spring. Since terminal resting buds do not form, there are but two growth periods associated with the formation of each shoot: during the first, the bud scales are formed; and during the second, the foliage leaves appear.

THE GROWING POINT

Hanstein's classification of tissues into dermatogen, periblem and plerome has been discarded by several recent workers including Schmidt (1924) Rösler (1928), Kühl (1933), Zimmerman (1928), and Foster (1935). It was shown by Schoute's (1902) researches and literature review that the Hanstein conception is not applicable to the growing points of all plants, and that the three classic histogens, even when present, are of little morphological significance. Schmidt (1924) suggested the terms "tunica" and "corpus" as substitutes for the terminology of Hanstein. He defined the tunica as the external layer or layers of cells at the stem tip which do not ordinarily divide in the periclinal plane except during leaf initiation. The corpus included all of the remaining internal tissue in which divisions may occur in any plane. The general applicability of Schmidt's conception has been discussed by Foster (1935) and need not be repeated here. The terms "tunica" and "corpus" as defined by Schmidt, will be used in this paper. While these terms represent tissues discrete at the growing point, they imply nothing concerning the origin of the vascular and cortical tissues of the stem.

Numerous median or nearly median longitudinal sections of the growing point of *Morus* suggest that the tip consists of a two-layered tunica and a central corpus (figs. 2, 4, 5). Foster (1935) found a similar situation in *Carya*, and for clarity in discussion referred to the outer layer of the tunica as T-1, the inner layer as T-2. Foster's scheme will be utilized in the present paper. T-1 (outer tunica layer) is homologous with the dermatogen of

Hanstein, while T-2 (inner tunica or subepidermal layer) corresponds to the periblem.

An idea of the structure of the growing point and the behavior of the histogens may be obtained by a study of figure 2, which is a section through

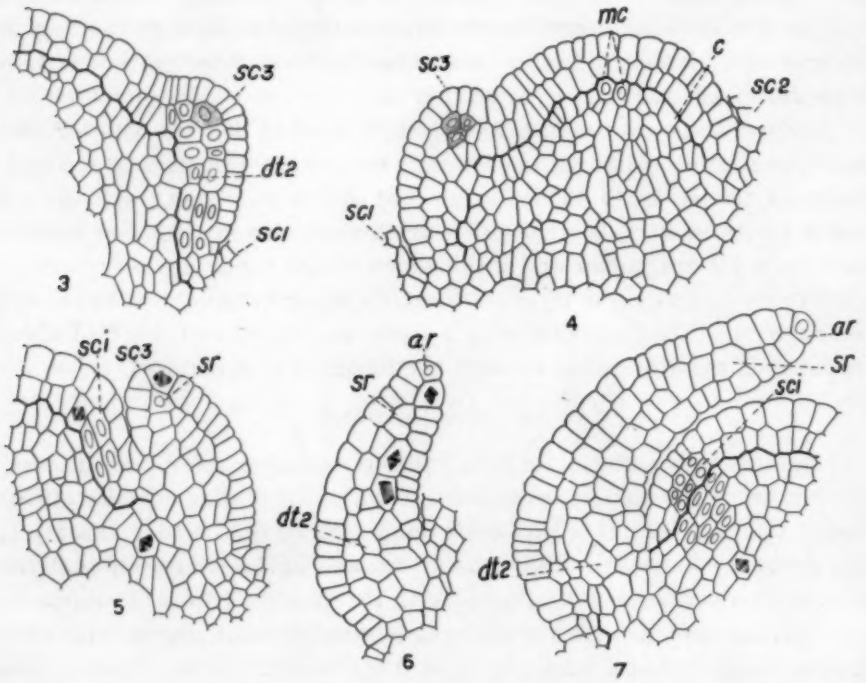


Fig. 3. Longitudinal section through portion of growing point and young bud scales; *sc3*, third scale (60μ high); *sc1*, first scale; *dt2*, inner derivative of T-2.

Fig. 4. Longitudinal section through stem tip and slightly older scales; *sc1*, first scale; *sc2*, second scale; *sc3*, third scale (70μ high); *c*, corpus; *mc*, initial cells of corpus.

Fig. 5. Longitudinal section through portion of stem and third scale (80μ high); *sc3*, third bud scale; *sci*, initial of fifth scale; *sr*, subapical row.

Fig. 6. Longitudinal section of a fifth scale (110μ high); *ar*, apical row; *sr*, subapical row; *dt2*, derivatives of T-2.

Fig. 7. Longitudinal section of a fifth scale (150μ high); *ar*, apical row; *sr*, subapical row; *sci*, initials of seventh scale; *dt2*, derivatives of T-2.

a stem tip that has been giving rise to foliage leaves. T-1 will be observed in every case as a discrete layer continuous over the stem tip and the young leaf at the left of the illustration. The independent origin and the exclusively anticlinal divisions of the cells of this layer are clearly evident. T-2 likewise occurs as a discrete layer, continuous over the stem tip beneath T-1, but at the left of figure 2 periclinal divisions in this layer have oc-

curred in connection with the formation of a young foliage leaf. Except during leaf or scale formation, periclinal divisions were never found in T-2 at the stem tip. In the internodal regions, however, periclinal divisions prevailingly occur in T-2, and the inner derivatives contribute to the cortex.

Beneath T-2 directly below the center of the stem tip in figure 2 will be observed a large pair of initial cells away from which the elements of the corpus diverge. From these large cells the outer one or two layers of the corpus may often be traced laterally to the base of the young leaf or bud scale, although periclinal and oblique divisions may occur at any time in the corpus, thus destroying the identity of the layers. It seems evident that the apical growth of the corpus is controlled largely by a pair or group of cells as evidenced by figures 2 and 4.

In some sections T-1 and T-2 seemed to diverge from respective groups of initials, but this behavior was not always evident as in *Carya*. In transection there may be frequently observed striking differences in size and staining reaction between the apical group of T-1 initials and the surrounding cells.

The activity of the corpus during foliage leaf initiation will be discussed in detail in a later paper. In figure 2, a procambial strand is forming to the left in the illustration, in the peripheral region of the corpus. This strand is formed in association with the young leaf, and will later become the median leaf trace. The trace differentiates basipetally until connection is established with the main vascular cylinder, and acropetally into the young leaf. Outside of the procambial strand the corpus gives rise to cortical tissue which will be augmented later between the nodes by derivatives of T-2. The central corpus becomes the pith.

THE INITIATION AND DEVELOPMENT OF THE BUD SCALE

The earliest evidence of bud scale initiation is shown by the appearance of periclinal walls in T-2 (figs. 5, 7). These walls first appear distinctly to the side of the growing point in the region that will later become the abaxial surface of the scale. In vertical section four or five cells finally appear to be active but this periclinally dividing layer in T-2 actually involves from one-third to one-half of the circumference of the growing point. The outer layers of the corpus also divide (fig. 7). Subsequent enlargement of the derivatives of the tunica and corpus results in the appearance of a bulge to the side of the growing point which in surface view appears as a crescent-shaped scale initial.

Figure 3 shows a longitudinal section of a portion of the stem tip and the third bud scale. For convenience a heavy dark line has been drawn to

delimit the tunica and corpus. The bulk of the young scale apparently consists of derivatives of T-2 which have enlarged considerably, although the corpus contributes slightly to the base of the scale. Near the abaxial surface one of the derivatives of T-2 has undergone a periclinal division; elsewhere only anticlinal walls have formed.

APICAL GROWTH OF THE SCALE

The method of growth of the scale immediately following the stage depicted in figure 3 may be seen by reference to figure 4. Near the tip of the scale in figure 3 is a dotted, subapical cell. In figure 4 this cell has apparently undergone two successive divisions—the first periclinal, the second anticlinal with respect to the surface of the primordium. Observations of many young scales indicate that divisions occur in this manner in nearly all scales and that subsequent increase in length is initiated by means of anticlinal divisions. In addition, the enlargement and division of the cells near the abaxial surface have resulted in a general increase in size of the young scale, and a decidedly greater curvature of the abaxial surface. The demarcation between the corpus and T-2 in the primordium is indistinct at this stage, but by carefully studying T-2 near the stem tip and by following this layer down into the young scale, it appears that the internal layers of cells of which the scale now consists have certainly been derived, mainly, if not entirely, from T-2. This contrasts with *Carya Buckleyi* where Foster found that the internal region of the young bud scale consists of a core of tissue derived from the corpus.

Following the stage represented in figure 4, anticlinal divisions occur in the cells near the tip of the scale. This results in a rapid increase in length, without however, an increase in radial thickness. In figure 5 is shown a longitudinal section of a bud scale in which such divisions have occurred. The increased length is due entirely to activity in the epidermal and subepidermal cells, which in turn, are derivatives of T-1 and T-2 respectively. Thus most of the scale shown in figure 5 may be safely referred in origin to the tunica, although a line delimiting the derivatives of the tunica and corpus can no longer be drawn.

Near the tip of figure 5 is a large, triangular subapical cell. This cell (a derivative of T-2) is a member of a subapical row which is continuous over the tip from one margin of the scale to the other. The function of the subapical row in the growth of the scale may be seen by reference to figures 6, 7 and 8, where, by transverse divisions, the row has given rise to a plate-like core of tissue enclosed by the young epidermis. This plate-like core, especially conspicuous in figure 8, is continuous at the tip between the margins of the scale.

In the epidermal layer at the extreme tip of the scale depicted in figure 6 is a large cell easily distinguished from its neighbors. The cell thus represented is a member of an apical row which extends over the scale tip, and is continuous with similar cells on either margin. The behavior of the apical row is apparent from figures 6, 7, and 8, where a series of divisions have occurred which simulate closely the divisions characteristic of the wedge-shaped marginal initials in the leaves of many leptosporangiate ferns (Bower, 1889). The initials of *Morus* are wedge-shaped and five-sided. They have two main cutting faces, but they occasionally divide in a plane perpendicular to the edge and to the surface of the leaf. Divisions are not confined to the apical row since mitotic figures frequently appear in its derivatives (fig. 6).

There is thus developed a scale which in median longitudinal section may be divided into four parts (figs. 6, 7): (a) a basal portion several cells in radial thickness, probably derived entirely from the tunica; (b) a median portion four layers of cells in radial thickness, certainly derived from the tunica; (c) a region near the apex consisting of three layers of cells, i.e. the epidermal layers and the derivatives of the subapical row; and (d) the apical region, consisting of the derivatives of the row of apical initials. The basal portion (fig. 7) shows the beginning of periclinal divisions in the abaxial subepidermal layer. Increase in radial thickness occurs partially as a result of such divisions, and partially as a result of similar divisions in the adaxial subepidermal layer. It is worthy of note that the basal portion of figure 7 is approximately 60μ in height, measuring from the juncture of the abaxial epidermis with the main stem to the region where the young scale is four layers of cells thick.

The scale now increases rapidly in length, by divisions in the apical row, the subapical row, the derivatives of these rows, the epidermis, and the region described above as four layers of cells thick. Anticlinal divisions resulting in an increase in length apparently do not occur in the basal region. Figure 8 is a median longitudinal section of a young scale which has attained a height of about 300μ. Although the total length of this structure is double that of the scale shown in figure 7, the length of the thickened basal portion is about the same in both cases. This indicates that the bulk of the scale is derived from the parts above the thickened basal portion as shown in figures 6 and 7, in other words from those regions which had their origin in the tunica at the growing point. It will be noticed in figure 7, that the abaxial half of the scale grows more rapidly than the adaxial, and as a result the scale curves protectively over the growing point. There is no indication of procambial tissue in either the scale or its subtended nodal region at this stage.

Apical growth of the scale continues in the manner described above until a height varying from 350 to 500μ has been attained. At this time the apical row of initials, each member of which has functioned as an apical cell with two main cutting faces, experiences a change in mode of division.

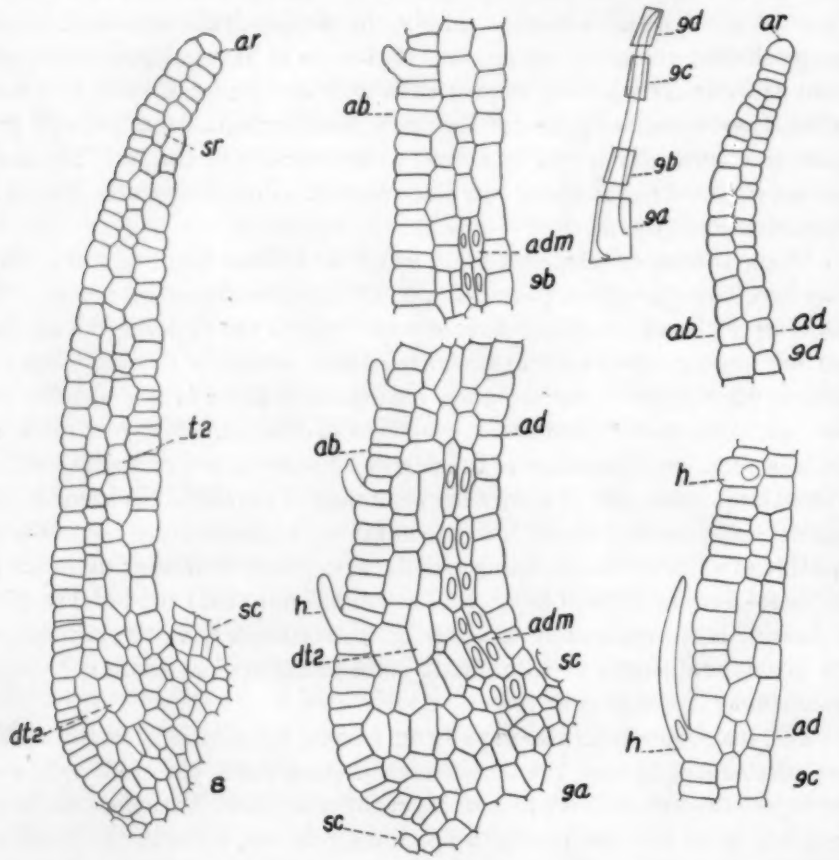


Fig. 8. Longitudinal section of a fifth scale (about 300μ high); *ar*, apical row; *sr*, subapical row; *t2*, derivatives of T-2; *dt2*, probably derivatives of T-2.

Figs. 9a–9d. Longitudinal sections at various levels in a fifth scale (about 750μ high); *sc*, scale; *dt2*, derivatives of T-2; *adm*, origin of adaxial meristem; *h*, hair; *ab*, abaxial surface; *ad*, adaxial surface; *ar*, apical row.

The new walls are laid down perpendicular to the longitudinal axis of the scale, and each member of the apical row produces a single chain of cells. The chains collectively form a sheet of tissue one cell thick at the apex (fig. 9d.) The amount of such tissue varies with individual scales. Since the apical row of initials is continuous with a similar row on each margin of the

scale, it might be expected that the marginal rows ultimately undergo similar changes in mode of growth, resulting in the formation of borders of tissue one cell thick which converge on the similarly constructed apex. Studies of cross-sections show this to be the case.

The basal portion of the scale (fig. 9a), i.e. the portion previously characterized as several layers of cells in thickness, gradually increases in length. This is due partly to the fact that its cells have enlarged, and to a limited extent, have produced new walls. However, the main way in which its limits have been extended is that periclinal walls have appeared in the internal layers of the region originally four layers of cells thick. The vertical extent of these periclinal walls is shown in figure 9a, where the divisions have occurred with greatest regularity in the adaxial subepidermal layer. The subepidermal dividing layer in figure 9a represents the origin of a cambium-like meristem, some of the derivatives of which later become the first vascular strands in the young scale. The periclinal divisions of the adaxial subepidermal layer gradually extend up the scale, and the region previously four layers of cells thick now consists of five layers (fig. 9b). In a similar manner periclinal walls occur in the median layer of the scale near the apex (fig. 9c). These walls usually appear near the center of the three-layered area and from this point are formed basipetally and acropetally (fig. 9c).

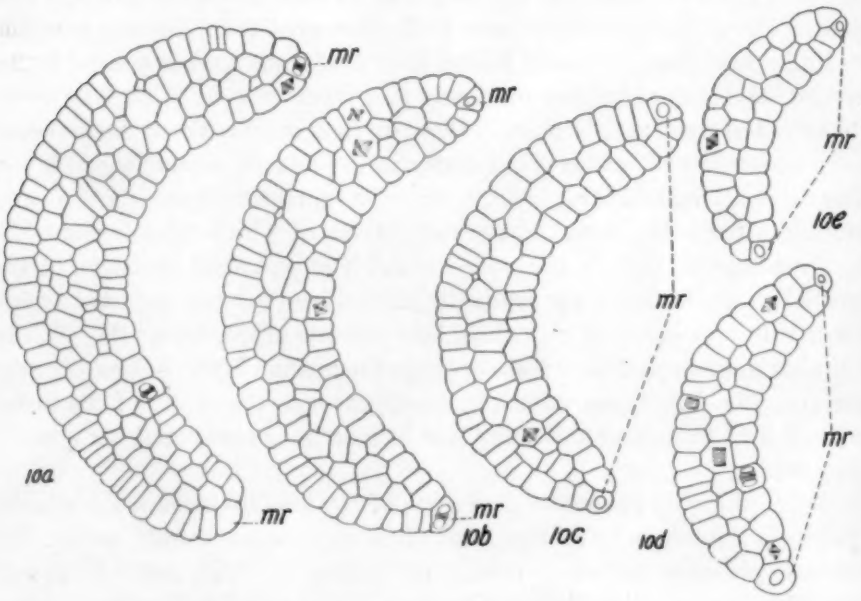
When the scale has reached a length of 500 to 600μ most of the adaxial epidermis has begun to mature, and divisions in it occur only rarely. The abaxial epidermis, however, retains the ability to divide actively as evidenced by the smaller, columnar nature of the cells, and by their dense protoplasmic contents. Numerous unicellular hairs are produced by the abaxial epidermis, a phenomenon which as suggested by Foster (1935) for *Carya* may be correlated with their active meristematic qualities. The hairs first appear near the median portion of the lower epidermis, but the area of their occurrence rapidly extends basipetally, acropetally and laterally. At maturity these hairs become quite stiff and appressed.

MARGINAL GROWTH OF THE SCALE

The method by which the young scale increases in width is practically identical with its mode of increase in length. Because of the tendency of the scale to curve over the apex of the stem, it is impossible to obtain perfect cross-sections of very young stages (figs. 4, 5). As growth proceeds, however, the scale becomes nearly erect due to the expansion of younger foliar organs, so that it was possible to obtain nearly perfect cross-sections of the 100–120μ stages.

Figures 10a–10e represent a series of cross sections of a scale approxi-

mately 120μ high. Reference to figure 10a reveals that the basal portion is nearly twice as broad as the scale is high. The lower margin is occupied by a large cell, somewhat similar in appearance to the cell seen at the apex of figure 6. The opposite (upper) margin is occupied by another such cell which is in the process of division. It is apparent that the new wall is being produced at such an angle that one of the daughter cells will resemble the

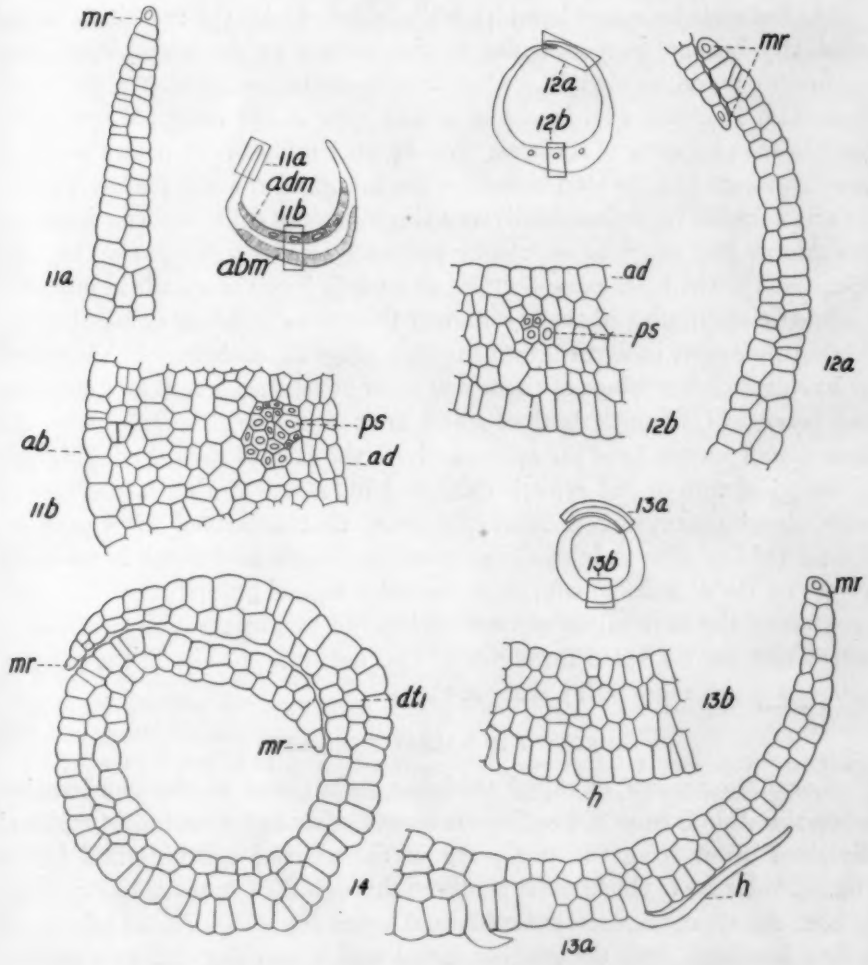


Figs. 10a–10e. Transverse sections at various levels of a third scale (about 120μ high); *mr*, marginal row.

wedge-shaped apical initials found at the scale tip. Twenty-five microns above figure 10a, and from there on to the tip of the scale, both margins possess well differentiated marginal initials (figs. 10b, 10c, 10d, 10e) which become continuous with the apical row. Thus the entire edge of the scale, from the base of one margin over the tip to the base of the other consists of a continuous row of wedge-shaped initials which adds to the width and height of the scale.

Immediately beneath the surface initial on each margin (fig. 10a) will be seen a large cell, clearly a derivative of T-2. Studies of serial sections (figs. 10b, 10c, 10d, 10e) show that such cells are members of submarginal rows which converge on the subapical row at the apex. The submarginal rows contribute to marginal growth in the same manner that the subapical row increases the vertical extent of the scale.

Since the submarginal and subapical initials of the scale primordium, in addition to the region previously described as four cells thick, may be traced in origin to the outer derivatives of T-2 (fig. 3), one may safely con-



Figs. 11a–11b. Portions of a transverse section about 20μ above the base of a fifth scale (about 850μ high); *ab*, abaxial surface; *ad*, adaxial surface; *ps*, procambial strand; *mr*, marginal row; *abm*, abaxial meristem; *adm*, adaxial meristem.

Figs. 12a–12b. Portions of a transverse section about 120μ above base of scale shown in figures 11a and 11b.

Figs. 13a–13b. Portions of a transverse section about 250μ above base of scale shown in figures 11a and 11b; *h*, hair.

Fig. 14. Transverse section about 500μ above base of scale shown in figures 11a and 11b; *dt1*, derivative of T-1; *mr*, marginal row.

clude that most of the scale, probably all of it, is to be regarded as a derivative of the tunica. However, since the demarcation between the tunica and corpus becomes indistinguishable at an early stage (figs. 4, 5) the possibility cannot be discarded that the corpus contributes slightly to the basal region.

As the scale increases in width walls laid down by the marginal initials gradually become perpendicular to the surface of the scale. When this occurs the marginal initials produce a narrow plate of tissue one cell thick (figs. 11a, 12a, 13a, 14). Divisions of this type in the marginal row occur later in the ontogeny of the scale than do the similar divisions in the apical row. In figure 11a the derivatives of the marginal row are plainly visible, first as a double layer and finally as a single layer of cells. The continuity of the double and single layers can be proven by a study of figures 11a, 12a, 13a, and 14, which are cross-sections at various levels of a scale about 650μ high. The continuity of the layers over the apex can be established by referring once more to figure 9d. At the 750μ stage the scale may be visualized as having an outer fringe of tissue one layer of cells thick and an inner area two layers of cells thick, both of which are continuous from just above the base of one margin over the apex nearly to the base of the other. The type of marginal and apical growth exhibited by *Morus* during late stages of scale development differs markedly from that described for *Carya* by Foster (1935). The scale of *Carya* grows in length and width in its early stages by the activity of subapical and submarginal groups of initials, augmented by the derivatives of more or less independent groups of dividing cells which are scattered throughout. This naturally results in the production of a much more bulky scale in *Carya*.

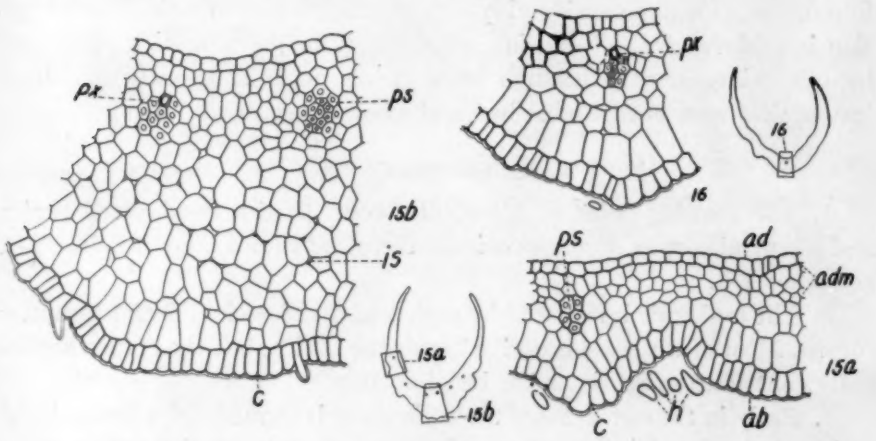
GROWTH IN RADIAL THICKNESS

Localized growth in radial thickness is initiated in the basal region when the scale is from 500 to 700μ in length, although occasional periclinal divisions occur from the beginning in the abaxial subepidermal layers (fig. 3). Increase in thickness is achieved through the cambium-like activity of both the ab-and adaxial subepidermal layers (fig. 11b). The adaxial layer is first involved, near the median, basal region, but the divisions rapidly spread both acropetally and laterally. Derivatives of the adaxial meristem contribute largely to the first formed vascular strands. These are initiated very late in the basal part of the scale (fig. 11b), differentiate acropetally and basipetally, and fuse irregularly in the cortex of the trilacunar node. Later, isolated strands appear farther up in the scale (fig. 12b), which differentiate acropetally and basipetally until they become continuous with the previously formed strands of the basal portion.

The scale is increased in thickness in the distal portions by periclinal division of the abaxial epidermal layer. Such divisions, however, occur

irregularly and produce isolated areas three layers of cells thick (figs. 13a, 14). Periclinal walls were never found elsewhere in the epidermal or T-1 layers.

The extent of meristem formation in the abaxial subepidermal layer varies with individual scales. The first four or five scales formed, grow considerably in this manner and have radially thickened basal portions. The inner scales, however, do not have conspicuously enlarged bases, and the activity of the meristems is reduced accordingly.



Figs. 15a–15b. Portions of a transverse section about 250μ above the base of a third scale (about 1000μ high); *is*, intercellular space; *c*, cutin; *px*, protoxylem element; *ps*, procambial strand; *adm*, adaxial meristem; *h*, hair.

Fig. 16. Portion of a transverse section about 510μ above the base of the scale shown in figures 15a and 15b.

Figs. 2–14 drawn at table level with Spencer camera lucida, under 2 mm. Leitz apochromatic objective, with periplan ocular 8×; reduced to one-fourth original size. Height given for young scales is the distance from the scale tip to the juncture of the abaxial surface and the main stem.

Figs. 15–16. Drawn and reduced as above, except with the use of a 4 mm. Leitz apochromatic objective.

The very late differentiation and maturation of vascular tissue are of interest since in these features the scales of *Morus* present a striking contrast with the situation in *Carya*. No trace of procambium was found in fifth scales up to 750μ high, and the first mature xylem elements were found in scales about 1000μ in height (figs. 15b, 16). In *Carya*. however, Foster found procambial tissue in the base of a scale 72μ high (op. cit. fig. 19a).

Detailed studies of the maturation of the scales were not made. In general this phenomenon is accompanied by the enlargement and vacuolation of all cells, particularly those in the abaxial portion (figs. 15a, 15b, 16). Intercellular spaces are conspicuous in scales 800μ high. A fully ma-

ture bud scale usually has from thirty-six to forty parallel, independent veins.

The walls of the epidermal cells thicken, and a layer of cutin is deposited over the abaxial surface. Stomata are formed in the abaxial epidermis. The cells of the abaxial subepidermal layer elongate in a plane perpendicular to the surface (figs. 15a, 15b), and in areas exposed to the air, become suberized.

During bud expansion in the spring, all of the scales except the outer four or five, elongate considerably and become photosynthetic. The elongation is achieved by cell division, particularly in the adaxial regions, and by cell enlargement. Although latex canals occur constantly in foliage leaves, they were not found in bud scales of any age.

SUMMARY

1. The growing point of *Morus alba* consists of a two-layered tunica and a central corpus. For convenience the outer tunica layer is called T-1, the inner T-2.

2. The bud scale is initiated by periclinal divisions in T-2 and the outer corpus. Most of the scale is derived from the tunica, but the corpus apparently contributes slightly to the basal portion.

3. Early in the ontogeny of the scale there is formed: (a) a bulky basal region, derived mainly from the tunica, but perhaps partly from the corpus; (b) a region four layers of cells in radial thickness, derived from T-1 and T-2; (c) a subapical row of initials derived from T-2; (d) a submarginal row of initials beneath each edge of the scale, derived from T-2, and converging upward to the subapical row; (e) an apical row of initials derived from T-1; (f) a marginal row of initials derived from T-1 and converging upward to the apical row.

4. All of the adult scale except a small median basal portion consists of derivatives of the apical row, marginal rows, subapical row, submarginal rows, and the region four cells in thickness. The original bulky base, the exact origin of which is somewhat in doubt, contributes little or nothing to the scale's apical and marginal growth. Thus the entire scale, with the possible exception of a basal portion is a product of the *tunica*.

5. The activity of the apical and marginal initials is strikingly suggestive of the mode of growth common in the young lamina of leptosporangiate ferns.

6. Vascular tissue differentiates very late, when the scale is 800–900μ in height. It forms as isolated strands which differentiate acropetally and basipetally.

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Germination of the resting spores of Diplophlyctis intestina

J. S. Karling

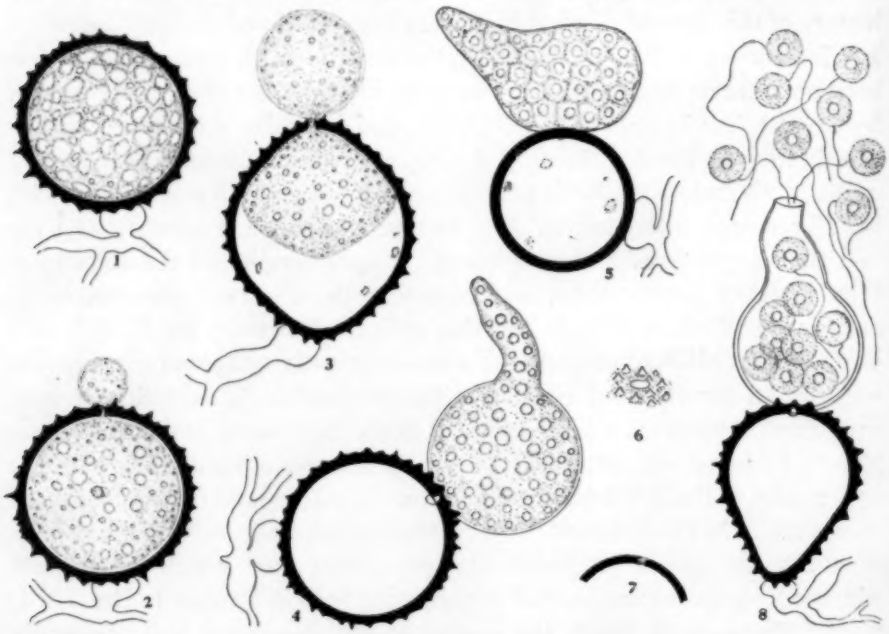
(with eight text figures)

Since the time *Diplophlyctis intestina* (Schenk) Schroeter was first discovered by the author in species of American Characeae in 1928, continual observations have been carried on to determine the method of germination of its resting spores and to complete our knowledge of the life history of this chytrid. Such spores occur in great abundance in dead nodes and internodes of *Chara*, *Nitella*, and other stonewort genera, and as has been proven experimentally serve as sources of infection from disintegrated host tissue. Yet in spite of this evidence, and extensive attempts to induce germination by freezing, heating, drying, etc., the results have been largely negative. Occasional isolated and empty spore cases with adhering vesicles have been seen from time to time, but because of their scarcity and the fact that no progressive developmental stages were found the author has been hesitant in describing and reporting the observed phenomena as universal and characteristic for this species. However, on New Year's Eve, 1935, myriads of resting spores in all successive stages of germination were found for the first time, and the process could be followed with comparative ease in the living material. Since that time germinating spores have been found almost at will, primarily because of familiarity with the appearance of the developmental and mature stages, and these subsequent observations have confirmed in every detail those made on New Year's Eve.

What the special environmental conditions were which led to such widespread germination at that time has not been determined. The *Nitella flexilis* filaments in which the resting spores developed had previously been killed by immersion in hot water for an hour, inoculated and allowed to stand in a small battery jar on a table near an eastern window in the laboratory. Within four days most of the algal filaments became heavily infected, and after a week resting spores were present in great abundance. Germination occurred approximately a month later. During this time the morning sunlight frequently fell directly on the culture for a few hours, and in the course of the nights the temperature in the laboratory often dropped below 50°F. during December. The culture was thus subjected to varying degrees of temperature and light intensity. Subsequent observations have led the author to believe that germination is rather common under ordinary laboratory conditions, and that such an environment is fairly optimum. Furthermore, the data at hand suggest, at least, that under such conditions the spores germinate very shortly after maturing, without

any prolonged resting period. Whether or not there is a definite periodicity out-of-doors has not yet been ascertained.

As has already been described by Zopf (1884), Sparrow (1932) and myself (1928) the majority of resting spores have a thick, brown, warty or spiny outer wall, although occasional smooth ones may be found. Whether or not the latter character is specific and we are dealing with more than one species has not been definitely determined. The content in the resting state is usually coarsely granular, with the granules and globules of such size and abundance and so closely crowded together that



Figs. 1–8. Successive stages in the germination of the resting spores of *Diplophlyctis intestina*.

many of the spores frequently appear as if they had undergone cleavage into segments. The first marked visible change in germination is the gradual breaking up of these granules into successively smaller units, and their dissolution. As this goes on the remaining ones appear more and more separated, and it soon becomes apparent that they are embedded or suspended in a more or less optically homogeneous hyaloplasm. Figure 1 shows a comparatively early stage in which smaller granules or globules appear to have been split off from the larger ones and lie between them. These bodies decrease in size and number with the successive germination stages, figure 2, and at the same time the remainder of the protoplasm becomes more finely granular and hyaline.

Concurrent with these changes a comparatively small cylindrical opening or pore develops in the thick outer wall. This opening is usually quite small and varies only slightly in size, so that it may be readily overlooked in living material before the spore content begins to emerge. So far I have been unable to follow the stages of its development because of the thickness and opacity of the cell wall. It may occur at almost any place on the periphery of the spore, and in one instance it was found at the point of attachment of the apophysis. Figures 2, 3 and 7 show the pore in longitudinal section, while in figure 6 it is shown in surface view. Sometimes it may be wider on the outer surface and appear somewhat funnel-shaped; at other times oval. So far only a single germination pore has been found for each individual spore.

In figure 2 is shown a median longitudinal view of a spore in which the content is beginning to emerge. The emerging vesicle appears to be quite naked at this stage, and in general appearance it seems to be more or less hyaline or finely granular with a few minute suspended refractive globules. Whether or not it is surrounded by a definite membrane at this stage is difficult to determine in living material. A later stage is shown in figure 3 in which approximately half of the content has emerged. In this figure the suspended, hyaline, refractive globules are more numerous and somewhat larger. This difference, however, is hardly to be regarded as a developmental change, since the appearance of the bodies varies considerably in different spores in the same stage of germination. Sometimes the protoplasm at this stage contains a number of vacuoles, similar to those of the developing evanescent zoosporangia; but from observation of numerous cases I have come to regard extensive vacuolation as frequently concomitant with degeneration. As the protoplasm flows out and draws away from the wall of the spore, irregular granules, hyaline globules and other residue may frequently be left behind, as is shown in figures 3 and 5.

Gradual emergence of the protoplasm continues until the entire content of the resting spore has escaped to form a vesicle on the outside. This vesicle then becomes transformed into a zoosporangium. Figure 4 shows a comparatively late stage in which the zoosporangium has been completely formed. It possesses a definite wall and a large exit tube or sporangial neck, and contains a definite number of large spherical, refractive globules suspended in a finely granular and more or less hyaline background. The maturation of this sporangium is essentially similar to that of the evanescent zoosporangia formed earlier in the life cycle of this organism. The refractive globules seem to originate by individual increase in size and confluence of smaller droplets, and process of spore delineation is by progressive cleavage. As to shape these zoosporangia vary from

spherical to oval, tubular, elongated and slightly irregular. As a general rule, however, they do not show the same range of variation in size as the earlier evanescent zoosporangia. Their size is more directly proportional to that of the resting spore from which they are formed. The exit tube also varies in diameter and length, but it does usually grow to the extreme length that may frequently be found in the evanescent sporangia.

The zoosporangium shown in figure 4 is mature and ready to undergo cleavage. This process is distinctly progressive and not simultaneous. In sporangia lacking a large central vacuole the cleavage furrows generally begin at the periphery and progress inward, but when a vacuole is present they also may begin in the center and travel outward. These furrows orient themselves in such a manner that each segment or zoospore initial at maturity contains only one of the large hyaline, refractive globules, as is shown in figure 5. Shortly after cleavage is complete the tip of the exit tube bursts and the zoospores begin to emerge one after another (fig. 8). Their emergence, behavior, size, shape and structure are strikingly like those of the zoospores from the earlier evanescent sporangia. They are spherical, possess a single cilium posteriorly attached, a large refractive globule, and dart about with great rapidity. After a motile period varying from approximately thirty minutes to an hour and a half they gradually become quiescent, lose their cilium and germinate. A large percentage of them, however, may degenerate if conditions are not optimum for growth. Numerous germination stages have been observed, and this process also is similar to that of the earlier zoospores, as has been previously described by the author (1930). A germ tube is formed which penetrates the host cell wall and branches very shortly. These initial branches are the rudiments of the rhizoidal system, and as soon as it has been established an enlargement of the germ tube above the branches occurs. This is the *anlage* of the zoosporangium, and as it begins to increase in size another swelling is formed between it and the rhizoids, which eventually becomes the apophysis. As a result of this growth and differentiation the rhizoidal system becomes oriented on the apophysis immediately beneath the incipient zoosporangium. With subsequent development and maturity, the evanescent zoosporangium with uniciliate zoospores is formed.

It is obvious from the above description that germination of the resting spore of *Diplophlyctis intestina* is essentially like that of *Polyphagus Euglenae*, described by Nowakowski (1877b), Dangeard (1900) and Wager (1913), and that the spore as far as we know at the present time is fundamentally a cyst and prosporangium. Whether or not it is a zygote formed as the result of the union of two gametes has not been definitely determined. In my cultures of *Diplophlyctis* separate sporangia-bearing micro- and macrozoospores frequently occur, but fusion has not yet been ob-

served. In view of the increasing evidence for the widespread occurrence of heterothallism the natural assumption would be that they are male and female thalli and that the resting spore is a zygote, but until actual fusion has been observed this conception is purely hypothetical.

Our knowledge of the complete life cycles of the majority of rhizidiaceous chytrids is quite meager. In a large number of genera and species resting spores have never been found and in those where such structures are reported to occur very few germination stages have been observed. In the family Rhizidiaceae, to which our species belongs, germination of the resting spores has been reported, as far as I am aware, in only six other genera and species, including *Polyphagus Euglenae*, *Entophlyctis Vaucheriae* (Fisch, 1884), *Rhizidium mycophilum* (Nowakowski, 1877a), *Chytridium olla* (De Bary, 1887), *Zygorhizidium Willei* (Loewenthal, 1905), and *Rhizophidium ovatum* (Couch, 1932). In all these species with the exception of the last two the resting spore has been shown to function as a cyst of prosporangium, and germinates as in *Diplophlyctis intestina*.

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Five-leaflet poison oak

JAMES B. MCNAIR
(WITH TEXT FIGURES)

Five-leaflet poison oak (*Rhus diversiloba* T. & G. forma **quinquifolia** forma nova) (foliis 5-foliolatis) was not known to Torrey and Gray (1838) at the time that they first named the plant *Rhus diversiloba*. The first appearance of the plant in scientific literature is in 1890 in Brandegee's report of the plants of Santa Catalina Island.

To determine if 5-leaflet specimens had been collected previous to 1890 inquiries were sent to the following herbaria: the University of California, Berkeley, California; Pomona College, Claremont, California, (P); Los Angeles Museum of History, Science and Art, Los Angeles, California; University of California at Los Angeles, Los Angeles, California; University of Southern California, Los Angeles, California, (U. S. C.); Natural History Museum, San Diego, California; California Academy of Sciences, San Francisco, California (S. F.); Santa Barbara Museum of Natural History, Santa Barbara, California; Dudley Herbarium, Leland Stanford Jr. University, Stanford University, California; National Museum of Canada, Ottawa, Canada; University of British Columbia, Vancouver, Canada (B. C.); United States National Herbarium, Washington, D. C.; Field Museum of Natural History, Chicago, Illinois (F.); Gray Herbarium, Cambridge, Massachusetts; Missouri Botanical Garden, St. Louis, Missouri (M.); New York Botanical Garden, New York, N. Y. (N. Y.); Oregon State College, Corvallis, Oregon (O.); Academy of Natural Sciences, Philadelphia, Pa.; State College of Washington, Pullman, Washington; University of Washington, Seattle, Washington; and Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming. As a result of this correspondence 5-leaflet specimens have been located as follows:

California: "Throughout California" 1866, *A. Wood* (N. Y.); Little Chico Creek, Butte Co., April 1896, *Mrs. R. M. Austin No. 749* (M.); Santa Catalina Island, August 1922, *E. C. Knopf* (F.); N. E. side Moraga Ridge, Oakland Hills, Contra Costa Co., Nov. 1, 1925, *John Thomas Howell No. 1541* (S. F.); Big Tujunga Canyon, just below and east of dam, alt. 2500 ft., May 13, 1934, *J. B. McNair* (U. S. C.); Cobal Canyon C. C. C. Camp, alt. 1500 ft., spring 1935, *J. B. McNair* (P); Corvallis, Oregon, Oct. 1935, *Helen M. Gilkey* (O). The writer first noticed 5-leaflet poison oak along the Mt. Wilson trail north of Pasadena, January 5, 1917. Observed by the writer along trail 200 yds. below Opid's Camp, West Fork San Gabriel R., alt. 4200 ft. Dec. 8, 1935.

A VEGETATIVE OR ECOLOGICAL FORM?

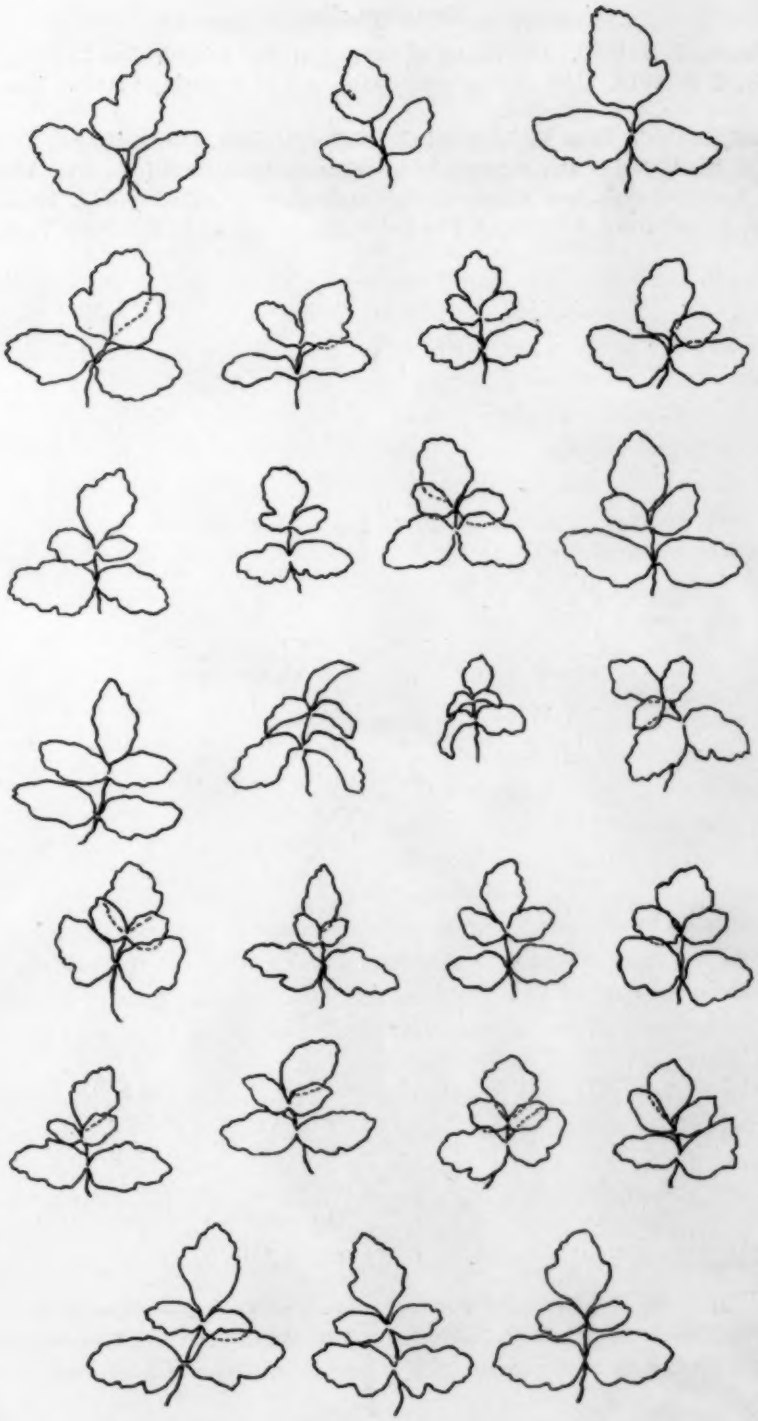
The question arises as to whether 5-leaflet poison oak is a vegetative or ecological form. The author cannot say what kind of soil or other conditions surrounded the specimens not observed nor collected by himself. But where he has observed these plants, plants of the 3-leaflet poison oak were found in the same localities. The author has found it only along the side of roads, trails or firebreaks. And in every case the plants on which the 5-leaflets are found have been cut back to their roots in an effort to kill them. In other words these plants may be considered as hedge or coppice forms produced by vigorous rapid growth. The conditions which bring about this 5-leaflet formation are therefore not ecological but vegetative. The plant consequently is a vegetative form. It seems best in order to prevent confusion with other plants to give this plant distinction as a form, *i.e.*, *Rhus diversiloba* T. & G. forma *quinquifolia*.

PHYLOGENY

A study of the plants which produce 5-leaflets shows that some of the plants have also 3- and 4-leaflet leaves as well as the 5-leaflet leaves. Some of the 3-leaflet leaves have very deeply incised lobes showing a marked tendency to form 4 and 5 leaflets as shown in text figures 1, 2 and 3. This tendency is no doubt caused by the increased vigor or energy of the plant due to pruning or cutting it back to the roots in an effort to destroy it. This supposition coincides with that morphological indicator of phylogeny compiled by Bessey (1915) which states that "simple leaves are more primitive than compound leaves." Or one can make a corollary under it to the effect that compound leaves with three leaflets are more primitive than compound leaves with more than three leaflets. This is shown not only in the case of 5-leaflet poison oak but in another one of the poisonous *Rhus*, namely *R. vernicifiua* Stokes (*R. vernicifera* DC.). Mobius (1899) found that in the sprouting seeds of this plant 3-leaflet leaves were first formed, to be followed by the usual compound leaves of 11–15 leaflets. Therefore, as ontogeny is a brief recapitulation of phylogeny (Haekel, 1906) we may say that in the poisonous *Rhus*, at least, the tri-foliate plants precede in evolution the plants with compound leaves which produce more leaflets such as the 7–13 leaflet *Rhus Vernix* L. (poison sumach).

Grateful appreciation is extended to the curators of the various herbaria who have assisted in this study by sending data.

Text figs. Outlines of 3-, 4- and 5-leaflet leaves of *Rhus diversiloba* T. & G. all collected August 13, 1935 by V. McAlmon and J. B. McNair at Cobal Canyon mouth, Claremont, Cal. $\times \frac{1}{6}$.



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Wound responses of Ficus australis

JOHN AUSTIN JUMP

(WITH SIX FIGURES)

Upon reviewing the literature on wound reaction and cicatrization of leaves, one gathers the impression that a leaf subjected to a traumatic stimulus will give a constant type of reaction if the conditions under which the experiments are performed are identical. Working with leaves of *Ficus australis* Willd. (*Ficus rubiginosa* Desf.) the writer has observed a number of variations in response, even in the same wound.

The outstanding publications on cicatrization prior to 1930 have been reviewed by Wylie (1930). The writer wishes however, to briefly mention certain papers that have a specific bearing upon this investigation. Massart (1898) notes that in foliar wounds on *Clivia miniata* Regel the neighboring cells proliferate and completely repair the wound. *Nuphar luteum* Sibth. & Smith was found to react by filling the large lacunae with proliferated cells in the vicinity of the wound. Gertz (1918) is reported by Wylie to have observed a marked hypertrophy of mesophyll cells bordering the tunnels of leaf miners. Blackman and Mathaei (1901) in an extensive investigation upon the wound reactions of *Prunus laurocerasus* L., find that the usual cicatrice is not formed when the material is kept moist in a beaker. Buscalioni and Muscatello (1911) were apparently the first to work with *Ficus australis*, but do not report the results that the writer has observed. Their paper is chiefly remarkable for the variety of methods which they employed in wounding many of the species which they enumerate. Krieger (1935) called attention to mesophyll proliferation and hypertrophy in *Ficus australis* but made no detailed study of it.

An understanding of the normal anatomy of the leaf of *Ficus australis* is necessary for the interpretation of wound reaction (fig. 1). The upper epidermis is multiple and heavily cutinized. The hypoderm consists of a layer of very large parenchymatous cells, one to two layers in thickness, in which occur idioblasts containing cystoliths. These idioblasts usually greatly exceed the normal hypodermal cells in size, and may be so large as to crowd out the layers of palisade immediately beneath. The palisade is double and contains numerous tanniniferous idioblasts which are usually confined to the upper and more compact layer of the palisade. The spongy tissue is very loosely organized and has large intercellular spaces. Tannin and latex occur in the spongy tissue, usually being found in more or less isodiametrical cells. Vascular structures show considerable variation, but the collateral bundle seems to be the most typical. Beneath the spongy tissue there is a low palisade, one cell in thickness, and a double layer of

cells composing the epidermis. The outer layer of this epidermis is composed of cells which are smaller and have thicker walls than those of the inner layer and is heavily cutinized. Stomata were found exclusively in the lower epidermis and sunken stomata are occasionally found.

The leaves upon which this study is based were wounded by cuts 4–12 mm. in length, using a sharp razor. The plant was approximately six years of age and grew in an unshaded position in one of the greenhouses of the University of Pennsylvania. The wounding was done during the late fall and winter months, and the leaves were allowed to remain upon the plant until collected for fixation. Material was fixed in Cohen's VIIc fixing fluid (1935) and stained in safranin and light green.

A few of the sections showed a definite cicatrice and pseudo-cicatrice, but in many cases a cicatrice failed to develop. In the latter instances the pseudo-cicatrice was usually either lacking entirely or only partially developed, and hypertrophied spongy tissue filled the intercellular spaces. As the proliferation of the spongy tissue continues, the new tissue fills the space caused by the wound and the surfaces of the wound are again organically united (fig. 3). In some cases one surface of the wound proliferates as described above, while the opposite surface cicatrizes (fig. 4).

When a cicatrice is not formed, the first reaction is the proliferation of cells in the spongy tissue. These cells are frequently hypertrophied and filled with granules of various size (fig. 2). The microchemical tests employed by the writer in attempting to determine the nature of these granules tended to indicate that they were derived from one of the constituents

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Explanation of figures 1–6

KEY TO LETTERING

ci, cicatrice; *cu*, cell from spongy tissue becoming cutinized; *cy*, cystolith; *dt*, dead tissue; *hd*, hypoderm division; *l*, latex cell; *ps*, pseudo-cicatrice; *ti*, tanniniferous idioblast; *x*, cells containing granules of undetermined nature; possibly a constituent of latex.

Fig. 1. Normal leaf structure.

Fig. 2. Beginning of proliferation of spongy tissue following wounding.

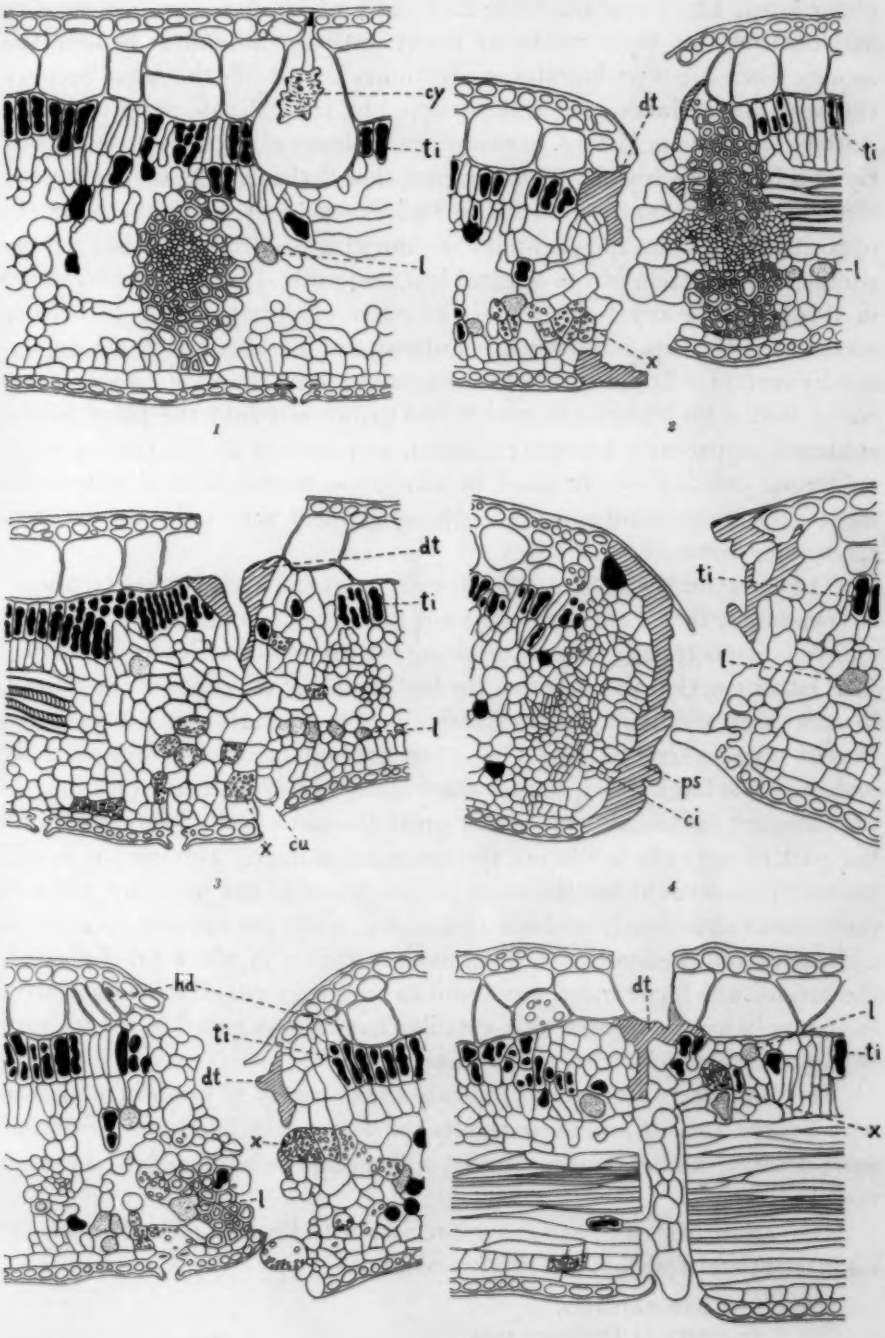
Fig. 3. Union of wounded surfaces. One of the cells of the spongy tissue in the region of the epidermis has secreted cutin on one side.

Fig. 4. Normal cicatrization on left surface of wound. Proliferation of cells with only a small amount of dead tissue on the opposite surface.

Fig. 5. Wounded section showing hypoderm becoming meristematic.

Fig. 6. Wound severing vascular bundle, showing spongy tissue filling the space between the cut ends of the bundle.

The sections illustrated in Figs. 2, 4, and 5 are all from the same wound and were fixed 32 days after wounding.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of the latex. The above reactions may begin within five days of wounding and continue for three weeks or more, until the wound is closed. The spongy tissue often proliferates so vigorously that it fills the space between the wounded surfaces ordinarily occupied by the palisade and hypoderm. Both of these latter tissues, however, were observed becoming meristematic in a few cases (fig. 5). This suggests that if the growth of the spongy tissue did not ordinarily proceed so rapidly, and insert itself between the opposite hypoderms and palisades, we might expect in some cases a more complete restoration of the original leaf structure. There was no evidence in this study of any tendency of the outer epidermal layers to become meristematic. There is, however, an attempt at a restitution of the epidermis by certain cells derived from the spongy tissue. In several cases it was noted that a mesophyll cell which had grown out into the plane of the epidermis apparently became cutinized, preparatory to functioning as an epidermal cell (fig. 3). In cases in which the wound severed xylem elements, the intervening space was promptly filled with cells derived from the spongy tissue (fig. 6).

The cause for these diverse reactions has not definitely been determined. It is apparent that if the razor does not make a clean cut there is considerable cell disintegration, usually resulting in a pseudo-cicatrice and cicatrice. This latter reaction also occurs if the leaf is young; the edges of the wound, in such cases, tending to gape excessively. When a mature leaf is wounded the cut surfaces tend to remain close together and usually become partially sealed by the latex which exudes abundantly and then dries. This may in part account for the absence of any great amount of cell disintegration on the part of the cells bordering the wounded surfaces. However it is still necessary to account for the cases in which one of the wounded surfaces proliferates abundantly without cicatrizing, while the opposite one forms a cicatrice and pseudo-cicatrice. In most instances in which this occurred, the surface which cicatrized was found to have been cut off from its nearest food supply by the wound, as a vascular bundle was found in the vicinity of the surface which failed to cicatrize (fig. 4).

The foregoing observations indicate the diversity of wound reaction in very limited areas. From these results the writer is inclined to believe that more detailed studies of other species will reveal similar unreported wound responses.

The writer wishes to express appreciation to Professor H. H. York for his interest and assistance in this investigation.

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